
1 m.1.


2 m.1


3. m.1.


4. m 2


5. p.m


6. m.1.


7. m.1


8. m 1.


9. m.2.


10. m 2.


11. m 1.


12. p.m


13. p.m.


14. m.1.


15. m.1.


16. m.1.


17. m.1.


18. m.1.


19. m.1.


20. m.2.


21. m.1.


22 m.1.


23. m.1


24. m 2.

E.C. & G.M. Woodward del. et lith.

Miocene & recent Sciuridæ.

West, Newman imp.

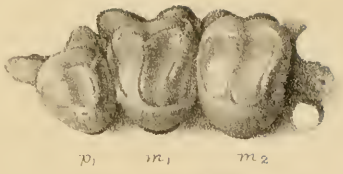
E.C.&G.M.Woodward del.et lith.

West, Newman imp.

Miocene & recent Sciuridæ.

1a 1b 1c

2. 3



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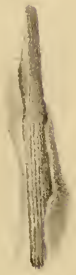

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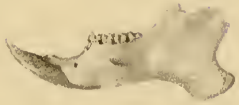

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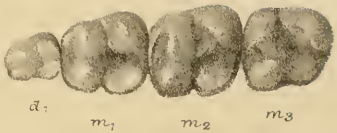

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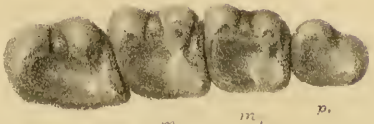

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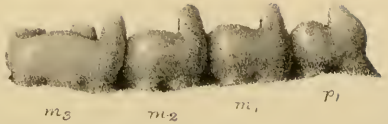

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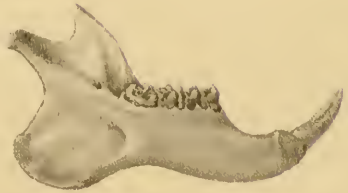
E.C.&G.M.Woodward del et lith

West, Newman imp

Miocene & recent Sciuridæ.



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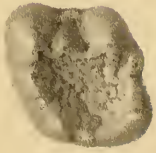

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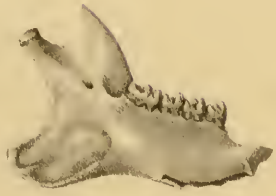

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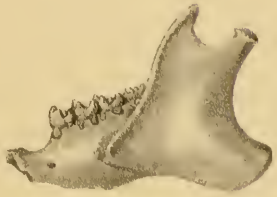

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E.C. & G.M. Woodward del et lith.

Miocene & recent Sciuridæ.

West Newman imp

1. On some Miocene Squirrels, with Remarks on the Dentition and Classification of the *Sciurinæ*. By Dr. C. J. Forsyth Major, C.M.Z.S.

[Received February 14, 1893.]

(Plates VIII.–XI.)

I. *Introduction.*

In order to determine some remains of Squirrels, collected by myself in the Middle-Miocene deposits of La Grive-Saint-Alban (Isère), it was necessary to compare them with their actual congeners. I have to thank both Dr. A. Günther and Mr. Oldfield Thomas for the kindness shown to me in permitting a close examination of the rich collection of Sciurine skulls in the Zoological Department of the British Museum; and I am besides under great obligations to Mr. Thomas, who is so thoroughly acquainted not only with every species, but indeed with every specimen of the collection under his charge, for having liberally favoured me with his experience and advice, especially in regard to intricate questions of synonymy and specific determination.

The investigation of living forms has led me somewhat farther than I had anticipated; so that before treating of the few fossil remains, it will be necessary to pass in review the numerous, and, in several instances, very unexpected forms of Sciurine dentition, as well as to present some remarks on their classification.

The brachydont teeth of *Sciurinæ* presenting a very primitive type of Rodent molars, I was naturally led to consider them in the light of the prevailing theory, the so-called tritubercularity, the rodent molars having been traced, as those of other orders, to a trituberculate type. This forms the subject of the last part of my communication.

II. *On the Dentition of the* Sciurinæ.

It is a well-known fact that in various families of the Rodentia tubercular molars—which as a rule are brachydont—and laminated molars—which as a rule are hypsodont or rootless—are met with side by side in closely allied genera and in existing species, whilst in some other Orders we have to look among fossils for the more or less brachydont precursors of the living hypsodont forms.

It is equally well known, though not always called to mind,

that the laminated hypsodont molars generally begin tubercular, and the tubercular brachydont molars, when worn, become laminated. For instance: the unworn upper and lower molars of *Castor fiber* show us a somewhat tuberculate crown, in which at first sight it is not easy to recognize the well-known laminated pattern of the worn tooth of the Beaver; likewise, a much-worn molar of the brachydont *Cricetus* presents enamel-folds and islets, though, owing to the shallower and wider valleys, they appear less distinct than in the hypsodont molars, whose valleys are reduced to narrow but deep fissures; so that there is only a gradational difference between tubercular and laminated teeth.

The molar teeth of Sciuridæ are generally represented as tubercular. But, in surveying all the known forms, even restricting ourselves to the subfamily *Sciurinæ*, we meet with all possible intermediate stages between the decidedly hypsodont molars of *Eupetaurus* described by Thomas[1] and the utmost degree of brachydontism as shown by the molars of the Bornean *Rhithrosciurus* or the Myoxine-like teeth of the group of pigmy Squirrels.

First, as to Brachydontism and Hypsodontism.

The species of *Pteromys*, in a restricted sense, are on their way to become hypsodont; they lead over on the one side to *Eupetaurus*, and on the other to the more or less brachydont *Sciuropteri* (including *Pteromys tephromelas*, Günth., and *P. phæomelas*, Günth., whose molars are quite similar to each other and agree more with the *Sciuropteri* than with *Pteromys*).

The African Ground-Squirrels (*Xerus*), as well as the Oriental *Sciurus berdmorei*, Bly., present a curious form of semi-hypsodontism, inasmuch as the internal moiety of the upper and more or less the external moiety of the lower molars are more elevated vertically than the external moiety above and the internal below. Corresponding to the hypsodont part of the molar, we find on the inner side of superior molars a stout and elongate root, on the outer side two smaller and shorter roots.

A small group of Ethiopian Squirrels included in the genus *Sciurus* (*Sc. palliatus*, *cepapi*, *pyrropus*, *congicus*, &c.) present a similar semi-hypsodonty, whilst the Moroccan *Xerus getulus* is in a lesser degree semi-hypsodont.

This greater vertical elevation of the inner side of the crown in superior, and of the outer side in inferior molars, though more evident in semi-hypsodont teeth, is, however, by no means limited to them; we meet with it, although in a lesser degree, in *Sciurus vulgaris* and its allies, and even in the still more brachydont *Rhithrosciurus*. *Ornithorhynchus* itself, as shown by one of the figures published by Stewart[2], has the inner side of the superior teeth more elongate than the outer. This cir-

[1] Oldfield Thomas, "On *Eupetaurus*, a new form of Flying-Squirrel from Kashmir," Journ. As. Soc. Bengal, vol. lvii. ii. no. 3, 1888, pp. 256–260.

[2] Ch. Stewart, "On a specimen of the true teeth of *Ornithorhynchus*," Micr. Journ. vol. xxxiii. n. s. 1891, pl. viii. *i*.

cumstance is of no small importance, as I shall have to point out later on.

The Common Squirrel, and many Oriental members of the genus, as well as some Ethiopian Squirrels (*Sc. rufobrachiatus*, Waterh., *annulatus*, Desm., *shirensis*, Gray, *punctatus*, Temm.), show relatively prominent cusps, and present a transitional stage between semi-hypsodontism and brachydontism. Still more brachydont are two other groups which have little affinity with each other—the African *Sc. stangeri*, Waterh., *Sc. ebii*, Temm., *Sc. aubinnii*, Gr., and the Oriental Giant Squirrels (*Sc. bicolor*, *indicus*, *macrurus*, &c.).

The Oriental Pigmy Squirrels (*Sc. exilis*, Müll., *Sc. melanotis*, Müll. & Schl., *Sc. concinnus*, Thos. (Plate X. fig. 10, Plate XI. fig. 7), *Sc. whiteheadi*, Thos.), as well as the pigmy Ethiopian *Sc. minutus*, Du Chaillu (Plate XI. fig. 6), show a low, oval-shaped and nearly horizontal crown, slightly concave in the middle, with transverse ridges. On the whole, their dentition has scarcely anything to do with the Sciuromorphous type of molars, and can only be compared with that of the Myoxidæ, *Eliomys* and *Graphiurus*.

Next we have to consider the pattern of the molars in *Sciurinæ*. The numerous modifications—almost every species presents some peculiarity—may be arranged under three heads:—

1. The first type is represented by the most brachydont forms: some Eocene Squirrels, as *Sc. spectabilis*, Maj., from Egerkingen, the Bornean *Rhithrosciurus* (Plate IX. fig. 2), the Oriental Giant Squirrels (Plates VIII. and IX. fig. 1), the Ethiopian *Sc. stangeri* (Plate VIII. fig. 7, Plate IX. fig. 7) and its allies, *Sc. ebii* and *Sc. aubinnii* (Plates VIII. and IX. fig. 8).

2. The second type is represented by *Sc. vulgaris* and its ally *Sc. syriacus* (I have had no opportunity of examining the dentition of the Japanese *Sc. lis*), by most of the Oriental middle-sized Squirrels (*Sc. prevosti* (Plate VIII. fig. 2), *Sc. lokroides* (Plates VIII. and IX. fig. 3), &c.), by a small Ethiopian group (*Sc. shirensis*, *Sc. annulatus*, *Sc. punctatus*, *Sc. rufobrachiatus*), and by most of the American Squirrels.

3. The third type is represented by several groups of Ethiopian Squirrels: *Xerus* (Plates VIII. and IX. fig. 10), including the Moroccan *X. getulus* (Plates VIII. and IX. fig. 9), by *Sc. cepapi* (Plate VIII. fig. 22, Plate IX. fig. 23), *Sc. palliatus*, *Sc. pyrropus* (Plate VIII. figs. 15, 23, Plate IX. figs. 15, 22), *Sc. congicus*, *Sc. leminiscatus*, *Sc. isabella* (Plates VIII. and IX. fig. 24), *Sc. loehmii*; as well as by some Oriental forms, *Sc. berdmorei* (Plates VIII. and IX. figs. 16–18), Gray's genus *Rhinosciurus* (Plates VIII. and IX. figs. 11, 12), &c.

I do not consider for the present the African and Oriental Pigmy Squirrels, as the characters of their dentition depart entirely from the Sciuromorphan type as a whole.

Brachydontism in itself is quite generally admitted to be the most generalized condition, and the teeth point in the same direction as do those of other Orders, viz., towards a still more primitive type. Besides, we are able to show that the two other

types before mentioned—the *Sciurus vulgaris* and the *Xerus* types, as we may call them—are each of them derived from a brachydont type.

1. Therefore, beginning with the type of the most brachydont Sciurine molar, as being the most generalized, the various forms belonging to it have a very flat elongate crown, the inner and outer sides of which have an almost equal longitudinal extension; and a minimum of transverse arrangement of their cusps, which show a tendency towards a longitudinal disposition.

2. In the upper molars of the *Sc.-vulgaris*-type a transverse arrangement is already conspicuous. The cusps have partly united to form transverse ridges, so that we see here the beginning of a transition from bunodontism into lophodontism: four more or less transverse ridges, the two median being the stoutest, with three intervening valleys. On the outer side are three prominent cusps, corresponding to the three anterior ridges. A characteristic feature on the inner side of the upper molars is an apparently single cusp, which fits into the cup- or basin-shaped hollow of the inferior molar, somewhat like a pestle in a mortar. In examining, however, quite unworn teeth (of *Sc. vulgaris*, e. g.), the inner side of the upper molar presents itself more elongate and shows a tripartite division, the median cusp being the stoutest. Still more is this seen in the upper molars of most of the middle-sized Oriental Squirrels, which in other characters (of the skull &c.) as well as in the dentition approach *Sc. vulgaris*. The molars, however, are somewhat stouter, and the cusps and ridges more prominent. In unworn teeth of Oriental forms, *e.g.* of *Sc. prevosti* (Plate VIII. fig. 2) or *Sc. lokroides* (Plate VIII. fig. 3), the inner margin is rather elongate, and shows more distinctly than does *Sc. vulgaris* the tripartite division with a prominent medial cusp. When the teeth have become somewhat worn, these divisions tend to disappear; so that the usual aspect of worn upper teeth in these Oriental Squirrels is that presented by the somewhat worn teeth of *Sc. vulgaris*, viz., a single broad internal cusp. The shortening, or, as one might say, the reduction and simplification of the inner side of the upper molars compared to the outer side (and, as may be added, of the outer side of inferior molars compared to their inner side) appears to be a general and primitive tendency of molar teeth; in fact, we meet with it already among Cretaceous Mammalia, as well as in the recent *Ornithorhynchus*. As to its meaning, we shall have to consider it afterwards.

In lower molars of the *Sciurus-vulgaris*-type, two cusps, the antero-external and the antero-internal, show a tendency to unite transversely. Anteriorly to these we have a small transverse valley, bordered in front by a transverse ridge, which is more rarely (*Sc. palmarum*) raised in two cusps. In the premolar there is generally one cusp only in front.

The hinder part of inferior molars is shaped into a sort of cup, to receive, as above mentioned, the internal tubercle of the upper

molars. This is a common form of inferior sciuromorph molar, as we meet with it, not only amongst most of the species of *Sciurus*, but as well in *Tamias*, *Spermophilus*, and *Arctomys*. The cup is bordered by the two anterior cusps, by two posterior cusps, of which the internal is generally less developed or suppressed, by a posterior heel, and sometimes by two secondary cusps between the two pairs of principal cusps. Sometimes the basin-shaped appearance becomes more evident still by the coalescing of all these cusps, so that already in quite unworn teeth, *e. g.* of the interesting *Sc. everetti*, Thomas (Plate IX. fig. 4), the rounded margin of the basin appears perfectly even.

In the *Sciurus-vulgaris*-type, the upper molars also present a sort of basin, in order to receive the postero-external cusp of the lower molars. This is the median valley, closed internally by the largely developed internal cusp, and whose formation appears to be due to the partial atrophy of a transverse series of cusps, there having remained only the internal one greatly developed, and often, as in *Sc. vulgaris*, a very small median cusp on the outer side. In the *Xerus*-type, to be mentioned hereafter, we frequently have the space of this median valley occupied by a transverse ridge, which brings up to five the number of these transverse ridges in the upper molars, with, between them, four narrow transverse depressions instead of three, as is generally the case.

The *Sciuropteri* come near to the same type, presenting on the whole a transitional stage between bunodontism and lophodontism, with the cup-like shape of lower molars, to which corresponds the formation of a median valley in the upper molars. In these last we find, moreover, the anterior valley of the crown more fully developed, than is the case in the members of the *Sciurus-vulgaris*-type, and thus the molars of *Sciuropteri* often present a more elongate form. A characteristic feature of Sciuropterine molars is a delicate wrinkling of the enamel of the valleys, and this, according to the different species, extends more or less to the cusps or crests, which thus appear crenate.

Lower basin-shaped molars are met with as far back as the Cernaysian fauna of Reims, the lowest known Eocene deposit in Europe [1]. This is one of the reasons which makes me agree with Schlosser [2] in considering the fossils (*Plesiadapis* and *Protoadapis*), described as Lemurids, to be Rodentia. The same conclusions, and for the same reason, apply to *Plesiesthonyx* from the "Faune Agéienne" of Reims [3], and to some specimens from the Eocene of Egerkingen, doubtfully referred by Rütimeyer to *Plesiadapis* [4].

[1] Lemoine, "Etude d'ensemble sur les dents des Mammifères fossiles des environs de Reims," Bull. Soc. géol. de France, t. xix. 1891, pl. x. figs. 64–68, 76–78.

[2] M. Schlosser, "Ueber die systematische Stellung der Gattungen *Plesiadapis*, *Protoadapis*, *Pleuraspidotherium*, and *Orthaspidotherium*," Neu. Jahrb. für Mineralogie, Geologie und Palæontologie, 1892, Bd. ii. pp. 238–240.

[3] Lemoine, *l. c.* pl. x. fig. 32.

[4] L. Rütimeyer, "Die Eocäne Säugethierwelt von Egerkingen," Abh. d. schweiz. paläontol. Ges. vol. xviii. 1891, pp. 121–125, pl. viii. figs. 16, 17.

3. To the *Xerus*-type belong most of the semi-hypsodont Sciurine teeth of the groups already mentioned. It is distinguished from the *Sciurus-vulgaris*-type by a more complete lophodontism, the crests running in a transverse direction, and the valleys being reduced to narrow but deep fissures. The main difference from Ungulate lophodont molars consists in their having not two, but four or even five crests, the anterior and posterior margin of the molar being as much or almost as much raised as the two medial crests. So that the *Xerus*-type presents in upper as well as in lower molars three transverse depressions or fissure-like valleys (and four in superior molars where there are five crests). This type forms on the whole a very striking approach to the hystricomorphan molar.

Twenty years ago I pointed out that two African Squirrels, *Sc. congicus* and *Sc. leucostigma* (this last being now considered as a variety of *Sc. pyrropus*), approach the Hystricomorpha in a further development of the characters in which the Ethiopian *Xerus* departs from the *Sciurus-vulgaris*-type. Again, the Eocene *Sciuroides* was shown to resemble in its molars those of the Hystricomorpha *Cercolabes* and *Erethizon*, whilst, on the other hand, the Eocene hystricomorphan *Trechomys* was shown to approach *Sciuroides*[1].

Twelve years later, Schlosser, working on fossil forms, with much richer material at his command, confirmed these observations, showing that a group of Tertiary Rodentia showed characters intermediate between the Sciuromorpha and Hystricomorpha[2].

It is of no little interest that actually living Sciuromorpha show in their dentition, as well as in the characters of their skull, that the distinction between Sciuromorpha and Hystricomorpha is less sharp than is generally admitted. Schlosser seems not to have examined any recent Ethiopian Squirrels, as he does not mention the important characters they present. Nor has any other author, with the exception of Alph. Milne-Edwards, who incidentally mentions *Sciurus pyrropus*, F. Cuv., saying that "les molaires offrent une apparence toute particulière, due à l'existence de replis d'émail qui s'enfoncent profondément dans la dentine, constituant ainsi de véritables rubans. Je ne connais que cette espèce sur laquelle on observe ces particularités ; cependant, chez certains *Xerus*, on en voit des indications "[3].

The fact is that the majority of Ethiopian Squirrels depart from the Sciurine type both in their superior and inferior molars, approaching towards hystricine lophodonty by the uniting of their cusps in a transverse direction, so that the characteristic cup-like

[1] C. J. Forsyth Major, "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz. Nebst Beiträgen zu einer vergleichenden Odontographie von Ungulaten und Unguiculaten," Palæontographica, Bd. xxii. 1873, pp. 75–130.

[2] Max Schlosser, "Die Nager des Europäischen Tertiärs etc.," Palæontographica, xxxi. 1885, pp. 19–162.

[3] H. et Alph. Milne-Edwards, "Recherches pour servir à l'Histoire Naturelle des Mammifères, etc." (Paris, 1868–1874), p. 166.

shape of inferior molars tends to disappear. The species which present in a greater or lesser degree this conformation are, besides *Xerus* (Plates VIII. and IX. fig. 10), including *X. getulus*, Gesn. (Plates VIII. and IX. fig. 9), *Sc. palliatus*, Pet., *Sc. cepapi*, Smith (Plate VIII. fig. 22, Plate IX. fig. 23), *Sc. pyrropus*, F. Cuv. (Plate VIII. figs. 15, 23, Plate IX. figs. 15, 22), *Sc. congicus*, Kuhl, *Sc. lemniscatus*, Le Conte, *Sc. isabella*, Gr. (Plates VIII. and IX. fig. 24), and *Sc. hochmi*, Reich. At the same time they present in their skull some resemblance to the Hystricomorpha. They also approach *Anomalurus* (Plates VIII. and IX. figs. 13, 14), the various hystricomorphine characters of which have long ago been noted, but have, I think, rather been underrated by Alston[1].

It thus would appear that we have here a group of Sciuromorpha, somewhat specialized in the direction of Hystricomorpha, as we find, too, in several Eocene Rodentia.

But this is not all. The molars of *Sc. berdmorei*, Bly. (Plates VIII. and IX. figs. 16–18), an Oriental Squirrel, and those of the Bornean "*Rhinosciurus*, Gr." (Plates VIII. and IX. figs. 11, 12), agree with those of *Xerus* and the above-named Ethiopian Squirrels, not only in their semi-hypsodontism, but likewise in their lophodontism, whilst the less semi-hypsodont Oriental *Sc. tristriatus*, Waterh., and *Sc. palmarum*, L., tend to connect the *Xerus*-type with the *Sc.-vulgaris*-type, in approaching the form of molar of most of the "middle-sized" Oriental Squirrels. Two other Oriental species, *Sc. insignis*, F. Cuv. (Plates VIII. and IX. fig. 6), and *Sc. hosei*, Thos.[2] (Plates VIII. and IX. fig. 5), from Borneo, though semi-hypsodont, and in other characters agreeing with the members of the *Xerus*-group, show a remarkable modification in the pattern of the molars, the valleys being reduced to mere superficial cracks, which disappear very early by wear. I think that we have in the molars of these two forms examples of that kind of retrogressive evolution of the molars to which attention has been lately drawn in an important paper by Leche[3], who attributes it to the modification of food. The *Macroglossi*, *Pteropus scapulatus*, and the *Epomophori*, differing in this respect from other *Pteropi*, feed on juicy fruits, whose contents need not be chewed. Likewise *Chiromys madagascariensis*, the molars of which present a similar kind of retrogressive evolution, is known to feed principally on succulent juices, especially of the sugar-cane, as well as on wood-boring caterpillars. It now is very suggestive that *Sciurus insignis*, according to Müller and Schlegel[4], is especially fond of juicy and aromatic fruits of different species

[1] Edward R. Alston, "On *Anomalurus*, its structure and position" (Proc. Zool. Soc. 1875, p. 94).

[2] Ann. Mag. Nat. Hist. for Sept. 1892, pp. 215, 216.

[3] W. Leche, "Studien über die Entwicklung des Zahnsystems bei den Säugethieren," Morphолog. Jahrbuch, xix. 1892, pp. 543, 544.

[4] Sal. Müller & Herm. Schlegel, "Over de tot heden bekende Eekhorens (*Sciurus*) van den Indischen Archipel," Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche Bezittingen," Leiden, 1839–44, p. 99.

of *Elettaria* (*E. mollis*, *speciosa*, and *coccinea*), as well as of some kinds of beetles and all sorts of caterpillars. A very similar food will in all likelihood hereafter prove to be preferred by *Sc. hosei*[1].

The molars of the semi-hypsodont *Pteromys* (Plates VIII. and IX. fig. 19) bear the same relation to those of *Sciuropterus* as the molars of the *Xerus*-type do to those of the *Sciurus-vulgaris*-type. In both, the valleys appear deepened and narrowed, but in *Pteromys* the narrowing is effected by the vertical increase of the wrinkles referred to in *Sciuropterus* molars (Plates VIII. and IX. figs. 20, 21, Plate IX. figs. 2, 5),—the result of which is that the cup of an inferior molar is filled up by these ramifications of the enamel, and the crown of both upper and lower molars becomes almost plane. The Eocene *Ailuravus* from Egerkingen (Switzerland)[2], which I consider to be a Rodent, is in this respect somewhat intermediate between *Pteromys* and *Sciuropterus*.

I have called the *Xerus*-type of molar a somewhat specialized one, and am justified in doing so, as the teeth presenting it are no more brachydont—brachydontism being the primitive condition. The brachydont crown of Sciuromorpha is at the same time bunodont; whereas the semi-hypsodont teeth are more or less, and the hypsodont teeth are completely, lophodont.

Another small group of Ethiopian Squirrels—*Sc. stangeri* (Plates VIII. and IX. fig. 7), *Sc. ebii*, and *Sc. aubinnii* (Plates VIII. and IX. fig. 8)—deserves the name of brachydont *Xeri*, as it shows from what form of brachydont molar the *Xerus*-type may have originated. Other characters of this same small group to be mentioned presently likewise point towards the Hystricomorpha, notwithstanding their perfect brachydontism.

In concluding these general remarks on the form of the Sciurine molar, I repeat what has already been stated, viz., that in perfectly brachydont Sciurine teeth the cusps tend towards a longitudinal arrangement—two marginal series in the lower molars: two marginal and one or more, more or less complete, intermediate series in the upper molars. This circumstance is of importance, as pointing towards the primitive arrangement of the molar cusps, and we shall have to revert to it when treating of the original type of molar.

III. *Remarks on the Classification of the* Sciurid.e.

We have now to consider some of the bearings of the foregoing remarks on Sciurine molars on Classification.

Classification was not my original purpose; but some of the results arrived at seem to me of some interest in this respect too, so that I think they may be worth mentioning. Nor do I see why

[1] Mr. Hose informs me that *Sc. hosei* is a ground-squirrel like *Sc. insignis*; this fact goes far to strengthen the supposition that the food of both is similar.

[2] L. Rütimeyer, *l. c.* pl. vii. figs. 18, 19.

systematic Zoology should not take into consideration, more than has been the case hitherto, the characters of the skull and dentition of Sciuromorpha, which characters have been of such excellent service for Myomorpha.

My arrangement of the Sciuridæ (see the table, p. 189) contains three subfamilies :—

1. *Sciurinæ*, including the genera of the subfamily *Sciurinæ* of authors (with the exception of the Flying-Squirrels and some pigmy forms), as well as the members of the subfamily *Arctomyinæ* (*Cynomys*, *Arctomys*, *Spermophilus*).
2. *Pteromyinæ*, including all the Flying-Squirrels (*Sciuropterus*, *Pteromys*, *Eupetaurus*).
3. *Nannosciurinæ*, the Oriental Pigmy Squirrels *Sc. exilis*, S. Müll., *Sc. melanotis*, Müll. & Schleg., *Sc. concinnus*, Thos. [1], *Sc. whiteheadi*, Thos. [2], as well as the Ethiopian Pigmy Squirrel, *Sc. minutus*, Du Chaillu.

I shall say a few words on the *Pteromyinæ* when dealing with the fossil forms.

As to my subfamily *Sciurinæ*, the inclusion of the *Arctomyinæ* in the subfamily *Sciurinæ*, which appears at first sight to be a radical change, will, I am sure, meet with the least opposition. The close relationships of *Spermophilus* to *Tamias* and *Sciurus* are generally recognized ; and my scheme is further justified by the consideration that several North-American species of the heterogeneous genus *Spermophilus* show in their skull and dentition a striking analogy with *Xerus*, a circumstance which has been generally overlooked. Besides, the dentition of the *Arctomyinæ* is so decidedly Sciurine that I do not see why we should any longer keep *Arctomys* and *Spermophilus* artificially separated from *Xerus* and *Sciurus*, for no other reason than convenience.

As to the minor divisions, it results from the preceding remarks on the dentition of *Sciurinæ* that the Ethiopian *Xerus* occupies, with its three species, a much less isolated position than has hitherto been admitted, inasmuch as numerous species of Ethiopian Squirrels, as well as some Oriental forms, included in the genus *Sciurus*, have close relations to *Xerus* in characters, which at the same time approach it to the Hystricomorpha. The characters of the skull of *Xerus* and its congeners point in the same direction, and consist, to express it briefly, in the elongate form of the cranium in general and the frontals particularly, coupled with the shortening of the postorbital processes ; whereas the remnant of *Sciurinæ* are, on the contrary, characteristic for their broad frontals and the long postorbital processes. Moreover, a small group of Ethiopian Squirrels, related to *Xerus* (*Sc. stangeri*, *Sc. ehii*, *Sc.*

[1] Ann. Mag. Nat. Hist., Nov. 1888, pp. 407, 408. *Hab.* Isabella, Basilan, Philippines.

[2] Ann. Mag. Nat. Hist. (5) 1887, xx. p. 127 ; P. Z. S. 1889, p. 231. *Hab.* Borneo.

aubinnii), presents a closer approximation towards the hystricine type in the relatively large infraorbital opening [1].

Again, another group of Ethiopian Squirrels (*Sc. rufobrachiatus*, *Sc. annulatus*, *Sc. punctatus*, *Sc. shirensis*), belonging to the *Sciurus-vulgaris*-type by the characters of their dentition, show in the conformation of their skull some approach towards *Xerus*; whilst, on the other hand, a few species, which from the form of their skull cannot be separated from the *Xerus*-group, tend by the characters of their molars somewhat towards the *Sciurus-vulgaris*-type, as, for example, amongst Oriental Squirrels the *Sc. tristriatus* and *Sc. palmarum*.

If we try to express by a systematic arrangement these various relations, two courses appear open to us: either to unite *Xerus* with *Sciurus*, or to create separate genera for those groups of species which depart from *Sciurus* in approaching *Xerus*. However, neither of these two suggestions seems satisfactory. By uniting *Xerus* with *Sciurus* this last genus would become still more heterogeneous than it is already—*Xerus*, sensu stricto, having besides near relationships with *Spermophilus*. By splitting up *Sciurus* in various genera, the relationships of these last to *Xerus* would not be seen in their true light. So that it appeared to me more rational to adopt a middle course, viz., to detach from *Sciurus* a certain number of species, which in their skull and dentition show Xeroine affinities, and to unite them with *Xerus*, which last genus would thus become composed of five subgenera (see the table on the opposite page).

The genus *Sciurus*, distinguished from *Xerus* by characters of the skull as well as of the dentition, is divided into three subgenera, each of which is characterized by cranial and dental peculiarities.

Subgen. *a*, *Exosciurus*, contains the Oriental Giant Squirrels, which by all authors on the subject, with the exception of Anderson, have been recognized to be a distinct group; in 1842 P. Gervais [2] pointed out the characters of the skull. As I have already stated more than once, the molars are perfectly brachydont, with delicate rugosities of the enamel-covering. Only one superior premolar.

In the subgenus *b*. *Sciurus* we have four divisions:—(α) A small group of Ethiopian Squirrels, characterized by the absence of the minute superior premolar, and, as a compensation, a very elongate posterior premolar. On the rest, the dentition is similar to that of *Sciurus vulgaris*. I have before described the slight differences in the molar pattern of division β, containing the majority of so-called

[1] Their skull in general, and most of all that of *Sc. ebii*, is so strikingly *Xerus*-like, with the only exception of the jugalia not being depressed, that it seems not possible to maintain them in the genus *Sciurus* if *Xerus* be maintained as such.

[2] P. Gervais, "Description de l'Ecureuil Delessert, accompagnée de quelques remarques sur la famille des Rongeurs sciuriens," Magasin de Zoologie, 2. iv. 1842, p. 4.

Fam. SCIURIDÆ.

I. Subfam. SCIURINÆ.

1. Genus Rhithrosciurus.
   Rh. macrotis, Gr.
2. Genus Xerus.
   a. Subgen. *Protoxerus*.
   X. stangeri, Waterh.; *X. ebii*, Temm.; *X. aubinnii*, Gr.
   b. Subgen. *Xerus*.
   X. rutilus, Cretzschm.; *X. erythopus*, Et. Geoffr.; *X. capensis*, Kerr.
   c. Subgen. *Atlantoxerus*.
   X. getulus (Gesn.).
   d. Subgen. *Paraxerus*.
   X. cepapi, Smith; *X. palliatus*, Pet.; *X. pyrropus*, F. Cuv.; *X. congicus*, Kuhl; *X. lemniscatus*, Le Conte; *X. isabella*, Gr.; *X. bohmi*, Reich.
   e. Subgen. *Eoxerus*.
   X. (*Rhinosciurus*) *laticaudatus*, Müll. & Schl.; *X. berdmorei*, Bly.; *X. tristriatus*, Charlesw.; *X. palmarum*, L.; *X. insignis*, Desm.; *X. hosei*, Thos.
3. Genus Sciurus.
   a. Subgen. *Eosciurus*.
   Sc. indicus, Erxl.; *Sc. bicolor*, Sparrm.; *Sc. albiceps*, Desm.; *Sc. macrurus*, Penn.
   b. Subgen. *Sciurus*.
   α. *Sc. rufobrachiatus*, Waterh.; *Sc. shirensis*, Gr.; *Sc. annulatus*, Desm.; *Sc. punctatus*, Temm.
   β. *Sc. erythraeus*, Pall.; *Sc. brookei*, Thos.; *Sc. tenuis*, Horsf.; *Sc. atrodorsalis*, Gr.; *Sc. rosenbergi*, Jent.; *Sc. caniceps*, Gr.; *Sc. ferruginens*, F. Cuv.; *Sc. lokroides*, Hodgs.; *Sc. prevosti*, Desm.; *Sc. steeri*, Günth.; *Sc. jentinki*, Thos.; *Sc. notatus*, Bodd.; *Sc. everetti*, Thos., *&c.*
   γ. *Sc. vulgaris*, L.; *Sc. syriacus*, Ehr.
   δ. *Sc. carolinensis*, Gmel.; *Sc. griseoflavus*, Gr.; *Sc. griseogenys*, Gr.; *Sc. æstuans*, L.; *Sc. deppei*, Pet.; *Sc. aberti*, Woodh., *&c.*
   c. Subgen. *Tamias*.
4. Genus Spermophilus.
5. Genus Arctomys.
6. Genus Cynomys.

II. Subfam. PTEROMYINÆ.

1. Genus Sciuropterus.
2. Genus Pteromys.
3. Genus Eupetaurus.

III. Subfam. NANNOSCIURINÆ.

1. Genus Nannosciurus.
   N. exilis, S. Müll.; *N. melanotis*, S. Müll. & Schleg.; *N. concinnus*, Thos.; *N. whiteheadi*, Thos.; *N. minutus*, Du Chaillu.

"middle-sized" Oriental Squirrels. Division γ, with *Sc. vulgaris* and *Sc. syriacus*, distinguished from each other by slight characters of the first superior premolar (p^1). Division δ contains most of the American Squirrels.

The third subgenus *c.* is *Tamias*, which I cannot separate from the genus *Sciurus*.

The skull of the Pigmy Squirrels is very remarkable, a fact to which attention has been drawn by Müller and Schlegel, as well as by O. Thomas. The anterior zygomatic root is a perfectly vertical narrow septum, and is placed so much backwards (above the second molar) that the facial part of the cranium appears very elongate, whilst the frontal region is broader relatively than in any other Sciuromorpha. The orbita is formed by an almost circular bony ring.

The dentition, of which I give the figures (Plate X. fig. 10, Plate XI. figs. 6, 7) is unique amongst Sciuromorpha, and can, as I have said before, be compared only with that of some *Myoxi*. In the upper jaw there are either one or two premolars, and one in the lower jaw. The posterior upper premolar (p^1) and the lower premolar (p_1) are of minute size as compared to the homologous teeth in other Sciuromorpha, sometimes scarcely one-third of the size of the molars. This is another feature they have in common with certain of the *Myoxi*. The pattern of the crown differs from that found in the Sciuromorpha generally, in presenting only three complete transverse crests in the upper molars instead of four, and three in the lower molars. The third crest, counting from front to back, of Sciuromorphous molars is very reduced in these pigmy Squirrels, sometimes scarcely more than a minute cusp. A further peculiarity of these molars is the large development of the anterior transverse valley of both superior and inferior molars, as compared to the usual Sciuromorphous type, sometimes almost equalling that of the posterior valley. This last, owing to the partial suppression of the third crest (Rütimeyer's *Nachjoch*), occupies the area of the median as well as that of the posterior transverse valley in the tooth of Sciuromorpha.

These characters of the teeth and the skull of the Pigmy Squirrels sufficiently justify the creation of a separate subfamily for them.

IV. *Description of the Fossil Species.*

The remains of two species of Squirrels are representatives, the one (1) *Sciurus spermophilinus*, Dep.[1], of the *Sciurus vulgaris*-type, the other (2) *Xerus grivensis*, n. sp., of the *Xerus*-type, which both types have been so fully discussed before, that I need scarcely enter into further details.

[1] Ch. Depéret, "Recherches sur la succession des Faunes de Vertébrés miocènes de la Vallée du Rhône," Arch. du Mus. d'Hist. Nat. de Lyon, t. v. (Lyon, 1887), pp. 108–110, pl. xiii. figs. 14, 14*a*.

Id., "La Faune de Mammifères miocènes de la Grive-Saint-Alban (Isère), etc.," Arch. Mus. d'Hist. Nat. de Lyon, t. v. (Lyon, 1892), pp. 48–50, pl. i. figs. 26–27.

Sc. spermophilinus is represented by a fragment of the left maxilla (Plate X. fig. 4), carrying the posterior premolar and the two anterior molars, and by several mandibular rami (Plate X. figs. 6–9). A minute alveolus for p_2 is visible in front of the posterior upper premolar. The inferior molars show the cup- or basin-shaped conformation, the cusps being arranged laterally.

Depéret is of opinion that the molars of *Sc. spermophilinus* differ from *Sc. vulgaris* only in small particulars. I find more resemblance to some Oriental members of the subgenus *Sciurus*; the antero-internal cusp of the lower molars being extremely elevated, whilst the postero-internal cusp is almost suppressed (Plate X. fig. 9). We meet with exactly the same pattern in the Oriental *Sc. atrodorsalis*, Gr., *Sc. rosenbergi*, Jent., *Sc. caniceps*, Gr., *Sc. brookei*, Thos., and others. The third lower molar is more elongate than in *Sc. vulgaris*; this, too, is a character of the Oriental group of Squirrels mentioned. Besides, both upper and lower incisors are vertically striated by ridges (Plate X. fig. 5). Amongst recent *Sciurinæ*, only *Rhithrosciurus*, whose molars, however, are very different from those of the fossil, presents this character. It occurs also on lower incisors of some species of *Sciuroides* from Cailux, in the British Museum. As the same striation of incisors is found in the Tillodont *Calamodon* of the Lower American [1] and Swiss [2] Eocene, it may prove to be an inherited character.

Length of m_2, m_1, p_1 sup., 6 millim.; length of m_3, m_2, m_1, p. inf., 7·5 millim.

Xerus grivensis, n. sp. (Plate X. figs. 2, 3).—A left mandibular ramus, showing the three molars and the alveolus of the premolar. Length of the three molars 6 millim. Incisor without vertical ridges. The molars present a more advanced stage of lophodontism than those of *Sc. spermophilinus*, not only the anterior cusps uniting transversely, but the postero-external and postero-internal cusp—the latter more fully developed than in *Sc. spermophilinus*—showing the same tendency. So that we have three, instead of two, transverse valleys, the median and posterior valley being incompletely divided. I could not better characterize the molars of this fossil than by calling them a minute and somewhat less semi-hypsodont form of *X. berdmorei*, Bly., from Martaban, Tenasserim, Cambodja, and Cochin-China.

Sciuropterus albanensis, n. sp.—The third fossil, a left ramus of the lower jaw (Plate X. fig. 1, Plate XI. figs. 3–5), is strikingly similar in the character of the molars and the ramus to some of the larger species of *Sciuropterus*, and especially to *Pteromys tephromelas*, Günth.[3] (Plate XI. figs. 1, 2), and *Pter. phæomelas*, Günth.,

[1] E. D. Cope, "The Vertebrata of the Tertiary Formations of the West," Book I. 1883 (Rep. Un. States Geol. Surv. of the Territ. vol. iii., Washington, 1884) pp. 188–192, pl. xxiv. c. fig. 1 *b*.

[2] L. Rütimeyer, "Die Eocäne Säugethierwelt von Egerkingen" (Zürich, 1891), pl. viii. figs. 25–27, p. 126.

[3] Proc. Zool. Soc. Lond. 1873, p. 413, 1886, p. 53.

from the Malay region and Borneo, which are both, from the conformation of their molars, not to be distinguished from *Sciuropteri*. I present an enlarged sketch of the fossil molars, together with the first molar of *Sc. tephromelas*. The few small differences shown by the comparison of the fossil with the recent species consist in a somewhat larger development of the anterior valley, and some minor details in the rugosities of the enamel. The cusps also, bordering the basin-shaped crown, are somewhat stouter in the fossil.

Length of the four grinders:—m_3 4, m_2 3·5, m_1 3, p_1 2·5 millim.

This is the first fossil of *Sciuropterus* recorded. However, I am of opinion that *Sciurus sansaniensis*, Lart., from the Middle Miocene of Sansan, is but a smaller species of *Sciuropterus*, judging, at least, from an enlarged figure of a molar published by Filhol [1].

Depéret has described and figured as a species of *Sciuroides* an inferior molar from the Lower Pliocene of Roussillon [2], which so much agrees with the homologous molar in some *Sciuropteri* (cf. *Sc. volans*), that I think I am right in considering the Roussillon tooth a third fossil form of *Sciuropterus*.

But this is not all: under the name of *Allomys* (*Meniscomys*), Marsh [3] and Cope [4] have made known remains of Rodentia from the Miocene of Oregon. Marsh considers them as "probably related to the Flying-Squirrels," adding that the teeth are somewhat like those of Ungulates.

Cope states [5] that "the characters of the dentition of this genus (i. e. *Meniscomys*) resemble those of the genus *Pteromys*."

The figures given by Cope are insufficient for close comparison, as has already been pointed out by Schlosser: but it would appear from the description that one of the species, *M. cavatus*, approaches *Sciuropterus* and especially *Sc. pearsoni*. The crowns of the inferior molars are described as basin-shaped; "and although the enamel is wrinkled in a complicated manner, the wrinkles are not elevated as in the other species of the genus. Thus the inferior molars more nearly resemble those of ordinary *Sciuridæ* than do those of the other species of *Meniscomys*" [6]. In the characters mentioned, these other species would form some approach to *Pteromys*.

When comparing the upper teeth of his *Allomys nitens* with those of Ungulates, Marsh doubtless refers to the angulate conformation

[1] H. Filhol, 'Etudes sur les Mammifères fossiles de Sansan' (Paris, 1891), pp. 36, 37, pl. i. fig. 3.

[2] Ch. Depéret, "Les animaux pliocènes de Roussillon." Mém. Soc. Géol. de France, Paléontologie, t. i. (Paris, 1890). p. 49, pl. vii. figs. 39, 39*a*, t. iii. 1892, p. 121, pl. xii. fig. 14. (The text quoted in the last instance refers to an upper molar figured, but there is no fig. 14 on pl. xii.)

[3] O. C. Marsh, "Notice of some new Vertebrate Fossils" (Amer. Journ. of Science and Arts, vol. xiv. 1877, p. 253).

[4] E. D. Cope, "The Vertebrata of the Tertiary Formations of the West." Book I. 1883 (Rep. Un. States Geol. Survey of the Territ. vol. iii., Washington, 1884).

[5] *L. c.* p. 827.

[6] *L. c.* p. 831.

of the outer cusps. A similar shape is shown by the outer cusps of *Sciuropterus pearsoni*, and by those of *Pseudosciurus*, which I have long ago[1] described at length, in drawing the attention to their various analogies with Ungulates. These analogies are so deceiving, that the discoverer of *Pseudosciurus*, having but isolated teeth at his command, considered them to be from an Ungulate.

Two lower molars of a Rodent from the Phosphorites of Mouillac have been described by Schlosser under the name of *Sciurodon*[2]. He compares them with *Pteromys*, and suggests that they are nearly related to, and perhaps identical with, the Oregon *Meniscomys*[3].

In the British Museum are preserved several unpublished isolated molars of a minute-sized Rodent from the Oligocene Bembridge Limestone of the Isle of Wight, some of which, likewise, can only be approximated to *Sciuropterus* or a nearly related genus. Similar remarks apply to a molar from the Swiss Eocene of Egerkingen, lately published by Rütimeyer under the name of *Ailuravus*[4], which, however, is undoubtedly a lower molar of a Rodent, and agrees most with those of the larger species of *Sciuropterus*, although, as stated above, it is somewhat intermediate between *Pteromys* and *Sciuropterus*. *Ailuravus* having relations to one of the species of *Plesiadapis* (*Pl. gervaisii*, Lem.), from the Lower Eocene of Reims[5], it results that *Sciuropterus*-like Rodentia were very abundantly represented and widely spread during the Tertiary.

I shall hereafter point out more fully the resemblance between two recent species of *Sciuropteri*, *Sc. horsfieldi* and *Sc. pearsoni*, with the two Eocene genera *Sciuroides* and *Pseudosciurus*.

After this brief reference to fossils showing close analogy with recent Flying-Squirrels, it remains for me to justify my arranging these last in a distinct subfamily, the *Pteromyinæ*.

Taking the genus *Pteromys* in a restricted sense, it is a very homogeneous one, in its dentition as well as in the characters of the skull. The *Sciuropteri*, on the contrary—with which I propose to unite *Pteromys tephromelas*, Günth., and *Pt. phæomelas*, Günth.—show on closer examination such a variety in the shape of their molars, that, if found in a fossil condition, they would without hesitation have been assigned to four or five genera. All of them are more or less brachydont, with the exception of *Sciuropterus volans*, L. sp., which leans towards hypsodontism; all have in common an elegant sculpturing of the enamel, which gives often a crenate appearance to the cusps or crests. But, apart from this, almost every species possesses a peculiar pattern of its molars.

[1] 'Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz,' 1873.

[2] M. Schlosser, "Die Nager des europäischen Tertiärs," *l. c.* pp. 91(73)–93(75), pl. vii. (ii.) figs. 3, 10.

[3] *L. c.* pp. 91, 146, 154.

[4] L. Rütimeyer, "Die Eocäne Säugethierwelt von Egerkingen" (Zürich, 1891), pp. 94–98. pl. vii. figs. 18, 19.

[5] Lemoine, "Etude d'ensemble sur les dents des Mammifères fossiles des environs de Reims," Bull. Soc. Géol. France, t. xix. 1891, pl. x. fig. 65.

Similar remarks apply to the skull. As to molar-forms, I draw attention to two of the most curious in this respect, those of *Sciuropterus horsfieldi*, Waterh. (Plates VIII. and IX. fig. 21), and *Sciuropt. pearsoni*, Gray (Plates VIII. and IX. fig. 20). The upper molars of both of these show, on the inner side, two crescents or cusps, with an intervening depression—a conformation which in recent adult Sciuromorpha is quite unique, but is met with in the Eocene genera *Sciuroides*, *Ischyromys*, *Pseudosciurus*. *Pseudosciurus*, moreover, though being somewhat more brachydont than *Sciuropt. pearsoni*, has in common with it the sculpturing of the enamel, as well as the pattern of the crown in general, there being six cusps in the upper molars, which in the living species show a tendency to form crests. *Sciuropterus horsfieldi* shows other relations to *Sciuroides*, besides those already mentioned.

Now, how are we to account for this astonishing variety of forms, which show this group in a new and unexpected light? The brachydontism for one thing proves that the *Sciuropteri* are old forms, and we have seen that they made their appearance certainly in the Middle Miocene in a form which has undergone very little change up to the present day, and that nearly related forms appear in the Oligocene of France and England, and in the Miocene of Oregon. Moreover, the nearest related fossil forms, of two of the species at least, are Eocene. In stating this, I do not pretend to say that *Sciuroides* and *Pseudosciurus* were Flying-Squirrels, but only that there is a near relationship between them and the two *Sciuropteri* mentioned.

Now, as to the genetic relation of the flying to the ordinary Squirrels, there are three suppositions possible:—

(1) The most obvious would be to admit that the Flying-Squirrels have evolved from various species of non-flying Sciuromorpha. In favour of this supposition it could be said that, considering Flying-Squirrels to be more specialized, they have apparently evolved from less specialized forms, and that the more favourable conditions in escaping their enemies might account for the survival of such forms as *Sciuropt. horsfieldi* and *Sc. pearsoni*, whose nearest relations were largely represented in the older Tertiaries. In support of a supposed independent evolution of the species of *Sciuropteri* from several species of *Sciuri*, the fact might be adduced that there exists some similarity in the dentition of an Oriental *Sciuropterus* (*Sc. fimbriatus*, Gr.) with several Oriental *Sciuri* (*Sc. prevosti*, e. g.); and the same might be said with regard to the Nearctic *Sciuropterus volucella*, Pall. sp., as compared with several Nearctic *Sciuri*.

(2) A second possible supposition would be the reverse of the first. For one reason or other, a patagium might have proved disadvantageous, and the *Sc. hudsonius* might be the descendant of such a form as *Sciuropt. volucella*, as *Sciurus prevosti* and other Oriental *Sciuri* might have sprung from some *Sciuropterus fimbriatus*. In favour of this supposition, the fact might be adduced that the species of *Sciuropteri* and *Pteromys*, taken together, are

inferior in number to the non-flying Sciuromorpha, and have, to all appearances, greatly diminished from Tertiary times up to the present, so that their special means of locomotion do not seem to have proved of more value in the struggle for existence to those of the non-flying.

(3) One may thirdly suppose that there is no direct connexion whatever between the *Sciuropteri* and recent *Sciuri* or *Sciuridæ*. From Tertiary times up to the present, the species of Flying-Squirrels have been gradually diminishing in number, their characters having proved inadaptive, whilst the species of Sciuridæ have been increasing. The points of similarity in the grinding-teeth of *Sciurus prevosti* and *Sciuropterus fimbriatus*, on the whole, are very slight (and so are those between *Sciuropterus volucella* and *Sciurus hudsonius*); with a little practice it is at once possible to distinguish an isolated tooth of the one from that of the other. Their skulls, moreover, are very different.

For my part, I rather incline towards the third supposition, although admitting that the grounds on which it is based may not be convincing. At any rate, the characters of the cranium as well as those of the dentition, though greatly varying, give on the whole a family likeness to all the Flying-Squirrels, so that I cannot but separate them into a distinct subfamily from the Sciurinæ.

The *Pteromys, sensu strictissimo*, have probably evolved from a single *Sciuropterus*-like form, and *Eupetaurus* is apparently the more specialized descendant of some *Pteromys*.

The really important characters in which some *Sciuri* and *Spermophili* approach the *Sciuropteri*, as in the restricted interorbital region of *Colobotis*, the general elongation of the frontals of various Sciuridæ, the general shape of the grinding-teeth in *Eosciurus*, and in the stronger development of the first ridge in the upper molars of the *Otospermophili*, are all such that they may be considered as ancient inheritances.

Therefore we need not admit any recent connexion between the *Sciuropteri* and the above-mentioned members of Sciuridæ.

Anatomical characters and palæontological evidence point in the same direction, viz. that the *Sciuropteri* are the little modified remnants of a very old and once widely spread group. There is not sufficient evidence for admitting that they have evolved from forms of non-flying Squirrels identical with, or very closely allied to, those actually living; their power of flying may not be a comparatively recent character. They are specialized, no doubt, compared to the remnant of Sciuridæ; but the ancestral non-flying types may neither have been Sciuridæ nor even Sciuromorpha.

It would be more consistent with these views to place the Flying-Squirrels in a distinct family; but for this it will be time enough when their recent as well as their fossil forms are better known than is the case at present[1].

[1] The present paper was completely finished when I first became partially acquainted with H. Winge's "Jordfundne og nulevende Gnavere (Rodentia)

V. *On the primitive Type of the Sciurine Molar, and of the Eutherian Molar in general.*

In surveying the various modifications of the Sciurine molar-type, I refrained from entering into the question as to their relation to the prevailing theory of trituberculism. I proceed now to this last part of my paper.

The tritubercular theory has been worked out with admirable acumen by Cope, Osborn, Schlosser, and lastly by Rütimeyer and Scott, and is so well known that I need not even give a summary of it. However, as I have to refer in the sequel to some less recent papers bearing on the argument, I may be allowed to mention them here as briefly as possible.

In a Memoir, which may be regarded to contain the foundations of a real comparative Odontography, Rütimeyer was led to consider as fundamental type of the Ungulate molar the zygodont form, viz. the upper molars formed by two transverse ridges, parting under right angles from an outer wall ("*Aussenwand*"), with a transverse valley dividing them, and two simple transverse ridges in the lower molars[1].

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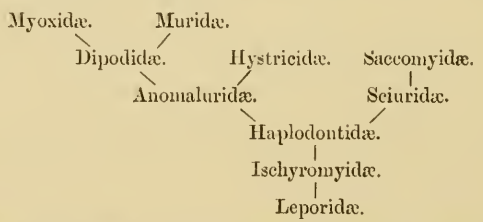
fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Gnavernes indbyrtes Slaegtskab" (Aftryk af "E Museo Lundii," Kjobenhavn, 1887). I regret not to have known this important publication before, but shall be obliged to take it into full consideration on the first opportunity if I succeed in overcoming the difficulties presented by the language. Meanwhile, at the risk of not having in every instance completely grasped the author's meaning, I cannot refrain here from a few observations. Winge presents (p. 110) the following genealogical tree of the Rodentia:—



Pseudosciurus and *Sciuroides* are included as a distinct subfamily under the Anomaluridæ, which last contain, moreover, besides *Anomalurus* (subf. *Anomalurini*), the Tertiary *Trechomys* (*Trechomyini*), *Theridomys*, *Issiodoromys*, *Archæomys* (*Theridomyini*), and the recent *Pedetes* (*Pedetini*). I do not in the least deny the importance assigned to the masseter (in its relation to the mechanical action of the teeth), and, as a consequence, to the shape of the infraorbital foramen. However, the agreement in the molars of *Sciuroides* with those of *Sciuropterus horsfieldi* on the one side, and of *Pseudosciurus* with those of *Sciuropterus pearsoni* (and to a lesser extent of *Allomys*) on the other, is such that I do not think it justified to separate so widely these fossil forms from the *Pteromyinæ*. Besides, amongst *Sciurinæ* proper, *Protoxerus*, my first subgenus of *Xerus*, still presents, in the conformation of the infraorbital foramen, some approach to the primitive condition.

[1] L. Rütimeyer, "Beiträge zur Kenntniss der fossilen Pferde und zur vergleichenden Odontographie der Hufthiere überhaupt," Verh. d. naturf. Ges. in Basel, iii. 1863, p. 558, gg.

Rütimeyer starts from the assumption that the primitive type of Mammalian molars had a conical or cylindrical shape ("*homœodont*" type), which simple form became complex in course of time, so that we must expect to find a more simple type of molars the more we recede in time. Rütimeyer's views were supported by the fact that, in several of the oldest deposits then known, of Tertiary Mammalia were met with abundantly the Lophiodontidæ, showing the zygodont molar in its typical form.

Kowalevsky[1] held the same views as Rütimeyer and pointed out, besides, that a less simply constructed form of molars is met with in the older Tertiary, especially amongst "primitive Ungulates" (e. g. "*Microchœrus*")[2]. But whilst he did not enter upon the possible relations between such complex sextubercular forms and the zygodont or lophodont type (as it was called later), Cope had urged already, in 1874, that a bunodont tooth was the ancestral form of the modern placental molar, thus tacitly admitting that the zygodont molar is a secondary, a derived form[3]. The various modifications of ungulate molars were traced back by Cope to a quadritubercular type, and somewhat later he traced the sectorial type of inferior molars to a quinquetubercular or tuberculosectorial type[4].

The discovery of the Puerco, the oldest known Tertiary Mammalian fauna of America, gave opportunity for the recognition by Cope of a still more primitive type of superior molar, the tritubercular type, the great majority of the Puerco Mammals having, according to Cope, their superior molars constructed after this type[5]. In the latest review of the Puerco fauna it is stated that almost all the Placentalia show the tritubercular type in their superior molars, as, out of 82 Placentalia, only four are quadrituberculate. The quinquetuberculate or tuberculosectorial type of inferior molars is equally widely spread, although less generally so, 64 out of 82 Placentalia possessing it[6].

The farther development of the tritubercular theory in these last years is treated of at length in all the recent Manuals, as the whole phylogeny of the Mammalia is directly connected with the question.

Not one palæontologist who has dealt with the argument has

[1] W. Kowalevsky, "Monographie der Gattung *Anthracotherium*, Cuv.," Palæontographica, xxii. 1873, 1874, pp. 210, 263, 264.

[2] "Je tiefer wir in die Schichten dringen, je ältere Formen wir finden, desto complicirtere Gestalten tauchen immer auf. . . . ; also kann das als ein Wink dienen, wie weit wir noch von der primitiven Form des Zahnes sind" (*l. c.* p. 230, note 1).

[3] E. D. Cope, "On the Homologies and Origin of the Types of Molar Teeth of Mammalia Educabilia," Journal Academy Nat. Sciences of Philadelphia, new series, vol. viii. part 1 (Philadelphia, April 1874), pp. 71–89.

[4] *L. c.* and E. D. Cope, "On the Tritubercular Type of Molar Tooth in the Mammalia," Pal. Bulletin, no. 97, Proc. Amer. Philos. Soc., Dec. 7, 1883 (publ. Jan. 2, 1884), p. 326.

[5] "On the Tritubercular Type &c.," *l. c.*

[6] E. D. Cope, "Synopsis of the Vertebrate Fauna of the Puerco Series," Transact. American Philos. Soc., Aug. 1888, p. 299.

pronounced unfavourably on the theory since it was first brought forth, and the same is the case, so far as I am aware, with biologists in general.

The cardinal point established, to use Osborn's words, is that "*the antero-external cusp in the lower molars and the antero-internal cusp in the upper molars of the Mammalia are homologous with the reptilian cone and with each other*"[1].

Trituberculism, or, as we rather ought to call it, the reptilian-cone theory, is no more a theory, but has become a dogma. I am a heretic, and may say that I opposed the theory already in 1873, viz. before it was invented[2]; since that time I have kept silent for various reasons.

My intention is not to deal fully with the subject on this occasion; I wish only to present a few general remarks on what I consider to be weak points of the theory, and then to enter on more particulars so far as the Sciurine type of molars is concerned.

It is but fair to begin with the Puerco fauna, the stronghold of trituberculism, from the discovery of which dates the establishment of the theory. In this fauna we have 106 species of Vertebrates[3], the most numerous being the Condylarthra with 23, and the Creodonta with 50 species[4]. I have already stated that, according to Cope, amongst 82 Puerco Mammalia only four are quadritubercular, all the rest being tritubercular.

Now it appears to me that the Puerco fauna, as at present known, does not give us an adequate idea of what must have been the Mammalian life of that period, the proportion of carnivorous Mammalia being far too large to be a real one. So that we meet here with exactly the same mode of argument which years before had been resorted to with regard to the zygodont type. In the oldest (then well-known) Tertiary Mammalian faunas the Lophiodontidæ, showing a relatively simple type of molar, were richly represented; hence it was concluded that this was the primitive type of the ungulate molar. Rütimeyer has recently strongly insisted upon the fact that the Carnivorous Mammalia of the Egerkingen fauna, the same which has yielded numerous remains of Lophiodontidæ, are exceedingly poorly represented, the remains of Ungulata being more than twenty times in excess of those of Carnivora[5]. In the Puerco, on the other hand, where we have an analogy to the Egerkingen[6] fauna in regard to primitive types,

[1] Osborn and Wortman, "Fossil Mammals of the Wahsatch and Wind River Beds, Collection of 1891," Extr. from Bulletin of the American Museum of Nat. Hist. iv. no. 1, Oct. 1892, p. 85.

[2] Forsyth Major, "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz. Nebst Beiträgen zu einer vergleichenden Odontographie von Ungulaten und Unguiculaten," 1873. Palæontographica, xxii.

[3] Cope, 'Synopsis Puerco Fauna,' p. 300.

[4] *Id. ib.* pp. 304, 305.

[5] L. Rütimeyer, "Die Eocäne Säugethierwelt von Egerkingen," Abhandlungen d. schweiz. paläontol. Ges. vol. xviii. 1891, p. 93.

[6] Rütimeyer, *ib.*

the proportion is reversed. The Creodonta, with, on the whole, a simple type of molars, prevailing in the Puerco fauna, this fact has been considered as conclusive for Cope's theory, that the Mammalian molar is derived from a tritubercular type.

Secondly, I cannot acknowledge that many of the Puerco molars said to be trituberculate, are really such; several species of *Mioclænus*, for example, showing a rather complex type.

Now, considering the fact that we meet amongst the so-called trituberculate types with molars which really are septem-, octo-, and novem-tuberculate, it would have been more correct to speak of a triangular type, this shape of the outline being the only thing the molars in question have generally in common. But they are not all even triangular forms, as those presented by "*Conoryctes*" *ditrigonus*[1], or *Periptichus rhabdodon*[2], show on either side of the principal inner cusp two secondary cusps, and Rütimeyer has recorded similar types from Egerkingen.

Moreover, Cope is not consistent with his own theory when he expounds his views as to the mutual relations of Creodonta[3]. The genus *Mioclænus*, from which all the other Creodonta are said to be derived, possesses the most complex structure of molar of them all; whilst *Mesonyx*, whose upper molars present a simple tritubercular type, is placed at the end of a series instead of the beginning, as the theory would require.

I further find inconsistencies in his diagram showing "the facts and hypotheses as to the phylogeny of the Mammalia"[4]. Here the Creodonta and Carnivora, as well as all the other placental Mammalia, with the exception of the Cetacea, are traced back by Cope to the Condylarthra. The latter, together with the Marsupialia, are derived from the Monotremata. This derivation implies that in the opinion of Prof. Cope the Monotrematous teeth must have been constructed on a trituberculate or a still more simple plan; and it may be remembered that when the first figures of worn teeth of *Ornithorhynchus* were published, they were proclaimed to support the tritubercular theory. But they are now known to be multituberculate; so I suppose that this being the case, the argument will probably be considered of no value, the *Ornithorhynchus* being an aberrant *Prototherc*. But still the fact remains, and we must deal with it, that the only prototherian teeth known to this day are multituberculate to the extreme.

If I am not mistaken, the above views of Cope as to the mutual relations of the different orders of Mammals,—views which are in opposition with tuberculism,—show that their author is on his way, unconsciously perhaps for the present, to become a partisan of the multituberculate origin of Mammalian teeth, so that support

[1] E. D. Cope, 'The Vertebrata of the Tertiary Formations of the West.—I.,' 1883, pl. xxiv. *d*. figs. 2, 4.

[2] *Ib.* pl. lvii. fig. 1 *a*.

[3] 'Synopsis Puerco Fauna,' p. 309.

[4] E. D. Cope, "On the Evolution of the Vertebrates, progressive and retrogressive," Amer. Naturalist, February, March, April, 1885 (printed April 13, 1884), p. 347.

seems to be coming to me from the very side from which it was least expected.

Schlosser in his turn has, in his elaborate and valuable Monographs[1], taken tritubercularism as his guide for tracing the phylogeny of various orders of Mammalia. He states his ground to be as follows:—"We have but to start from the perfectly recognized primitive type and to trace the modifications which it has undergone"[2]. This perfectly recognized primitive type is, according to Schlosser, the tritubercular type of upper molars, and the tuberculo-sectorial type of lower molars. Accordingly, in the diagram placed by him at the head of the Monograph of Carnivora[3], this form of molar type is attributed to the supposed first true Carnivore.

In accordance with the theory, Schlosser considers *Mesonyx* or *Sarcothraustes* to be the primitive type of Carnivora[4]. With the same inexorable logic all Ungulates are derived from carnivorous Mammalia; the Condylarthra being considered as intermediate between the Ungulata and Creodonta[5].

I have not to deal with Carnivora on this occasion, so that I will only mention incidentally that, in my eyes, amongst recent Carnivora, the Subursi (and, so far as the form of molars is concerned, *Ailurus*) approach nearest to the primitive carnivorous Mammalia, whilst some of the Arctocyonidæ are the most primitive of Creodonta.

Further objections may be made when Schlosser considers with Cope a rather complicated form of inferior molar—the tuberculosectorial type—to be a primitive form, and when it is assumed that, whilst the upper molars become further modified by addition, the lower molars from quinquetubercular become quadritubercular in progress of time, by the loss of an anterior cusp, the paraconid. The tuberculosectorial type is, in its turn, derived from a simpler

[1] M. Schlosser, "Beiträge zur Kenntniss der Stammesgeschichte der Huf thiere und Versuch einer Systematik der Paar- und Unpaarhufer," Morpholog. Jahrbuch, xii. 1887, pp. 1–136;—*id.* "Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten," I.–III., Wien, 1887–1890 (Beiträge z. Paläontologie Oesterreich-Ungarns, Bd. vi.–viii.);—*id.* "Ueber die Beziehungen der ausgestorbenen Säugethierfaunen und ihr Verhältniss zur Säugethierfauna der Gegenwart," Biologisches Centralblatt, Bd. viii. no. 19, Dec. 1888, pp. 582–631.

[2] "Es handelt sich nur darum, von dem wohlerkannten Grundtypus auszugehen und alle Veränderungen zu verfolgen, welcher derselbe fähig ist," Die Affen, &c. ii. p. 9 (233).

[3] *Id. ib.* p. 4 (228).

[4] "Wenn wir von der Voraussetzung ausgehen—und hiezu sind wir auch vollauf berechtigt—dass der *Oberkiefer-Molar* der Creodonta ursprünglich den Trituberculartypus in vollster Reinheit gezeigt habe, so müssen wir *Mesonyx* oder *Sarcothraustes* unbedingt als den Urtypus betrachten, wenigstens für jene Formen, deren obere Molaren mit *rundlichen* Höckern versehen sind. Es schliessen sich diese Typen mehr an die Raubbeutler als an *Didelphys* an," Die Affen, Lemuren, etc. i. p. 161.

[5] ". . . es kann keinem Zweifel unterliegen, dass alle Hufthiere von Fleischfressern abstammen, wobei eben die Condylarthren das Zwischenstadium repräsentiren"—M. Schlosser, Ausgestorbene Säugethierformen, *l. c.* p. 585.

form by the addition of the so-called *heel* or *talon* to the original trigon.

The name of *heel* or *talon* is borrowed from the teeth of Carnivora, where this part, as the name implies, generally appears in a reduced form compared with the rest of the tooth. In other orders the so-called *talon* is, as a rule, a well-developed part of the inferior molar, so that it seems *a priori* highly improbable to consider as a later development that part which, in the majority of Mammalia, constitutes the whole posterior moiety of the lower molars. What we at present know of the oldest forms of Perissodactyla, Condylarthra, Rodentia, and even of some forms of Creodonta, as revealed especially by the Cernaysian fauna of Reims[1], does not in the least justify a similar assumption. On the contrary, the "*talon*," far from showing a tendency to disappear, is in several of these archaic *Eutheria* very prominent, and even more distinctly developed than in any later form, not only in longitudinal extension, but partly even in the elevation of the cusps, as compared with those of the anterior moiety.

The question of the heel leads us to an objection made by Fleischmann, who on the whole accepts the tritubercular theory, but maintains that the cusps of upper molars are not directly homologous to those of the lower molars; or, in other words, that not only does the internal side of upper molars correspond to the external side of lower molars, as admitted by Cope and Osborn, but that, besides, the anterior part of upper corresponds to the posterior part of lower molars[2].

In reply to Fleischmann, Osborn states that "this objection would be fatal to a uniform system of nomenclature for the upper and lower cusps if it could be sustained," but that it is disproved by a comprehensive survey of the Mesozoic trituberculates, especially of the Amblotheriidæ and Spalacotheriidæ[3]. Neither Osborn nor Fleischmann seem to be aware that, if the latter *is* right, his objection will be fatal not only to the homology of upper and lower cusps, but also to the theory, for the primitive trigon which includes the protoconid, the supposed homologue of the reptilian cone, would in that case be found to be formed for the greater part by the very heel which the theory considers to be a late addition.

There can be no doubt as to the correctness of Fleischmann's statement, which is easy to verify. A left upper anterior milk-tooth of *Didelphys*, for instance, is at first sight very difficult to distinguish from one of the right lower series. Even in such specialized molars as those of modern Ruminants, in holding side by side a right upper and a left lower molar, or *vice versa*, what appear to be the mutual homologies are to be traced out even to

[1] Lemoine, "Etude d'ensemble sur les dents des Mammifères fossiles des environs de Reims," Bull. Soc. Géol. de France, iii^e série, t. xix. 1891, pp. 263–289, pls. x., xi.

[2] A. Fleischmann, "Die Grundform der Backzähne bei Säugethieren und die Homologie der einzelnen Höcker" (Sitzungsber. d. k. Preuss. Akad. d. Wiss. Berlin, 1891).

[3] Osborn and Wortman, *l. c.* pp. 84, 85.

very small details. The only inference I wish for the present [1] to draw from this fact and its consequences is, that Prof. Fleischmann, too, is on his way to become an opponent of tritubercularism.

It would appear that the Allotheria, the Multituberculata *κατ' ἐξοχήν*, ought to have been a stumbling-block for the theory. But this is not the case; they have been simply pushed aside on account of being an aberrant order. Nevertheless, I shall refer to them later on.

The dentition of Rodentia has as yet not much been dealt with in relation to the tritubercular theory. Scott was the first to touch upon the question, when describing the *Plesiarctomys sciuroides*, S. & O., from the Uinta formation[2], considered by him to be "one of the oldest, if not the very oldest known form of rodent." Owing to the importance which for this reason is attributed to the fossil, I must dwell upon the subject at some length. Scott has shown to his own satisfaction and to that of others that the superior molars of *Plesiarctomys sciuroides* "are plainly of the tritubercular pattern," and that "the inferior molars show the anterior triangle of three cusps with a talon behind, or what Cope has termed the tuberculo-sectorial molar." It might be questioned at once whether this specimen, the teeth of which are much worn according to the author's own assertion [3] and according to what appears from the diagram [4] and the figures [5], is a proper object from which to draw such important inferences. I fail to see in its molars anything else than the usual Sciuromorphine type, which I agree with Scott in considering as a very old one. I have myself pointed this out twenty years ago in some fossils (*Sciurus spectabilis*) from the Eocene of Egerkingen [6], which are rather older than the Uinta formation. The Uinta beds are considered by Zittel [7] to be Lower Oligocene, whilst the Bohnerz of Egerkingen has important relations with the oldest Eocene of Europe (Reims) and America (Puerco)[8]. On the other hand, this type is still in existence, and widely spread among living Sciuromorpha.

I think that Scott is mistaken in what he considers to be the homologies, in the lower molars of *Plesiarctomys*, of the anterior triangle of Ungulates, Creodonts, and Lemuroids. This anterior triangle is formed, as clearly shown by unworn molars of most of the Sciuromorpha, by the antero-external and antero-internal cusp (the *protoconid* and *metaconid* according to Osborn's no-

[1] See also W. B. Scott, "The Evolution of the Premolar Teeth in the Mammals" (Proc. Ac. Nat. Sci. Philad. 1892, p. 410).

[2] William B. Scott and Henry Fairfield Osborn, "The Mammalia of the Uinta Formation" (Trans. Amer. Philos. Soc. n. s. vol. xvi. pt. iii. Aug. 20, 1889, pp. 476–478).

[3] *L. c.* p. 477.

[4] P. 476.

[5] Pl. xi. 1 *c*, 1 *d*.

[6] Forsyth Major, "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz."

[7] 'Handbuch der Paläontologie, I. Paläozoologie,' IV. Band, 1892, p. 66.

[8] L. Rütimeyer, "Die Eocäne Säugethierwelt von Egerkingen," Abhandl. schweiz. paläont. Ges. xviii. 1891.

menclature)[1] more or less transversely united, together with Osborn's *paraconid*[2], and include between them what I have called the anterior transverse valley. Owing to the much-worn condition and partly too, perhaps, to the feeble development of this anterior part—as found in some recent *Sciuri* and in *Arctomys*—the anterior valley has vanished in the fossil molars, though I think that some traces of it are still visible in the first and third molar of Scott's figures[3], so that, in order to find out the typical triangle, Scott has encroached on what trituberculism declares to be a late addition to the inferior molars, for he considers, as it were, the postero-internal cusp, Osborn's *entoconid*, of the "heel" to be the postero-internal part of the typical triangle. What he calls the talon behind, is but the median cusp (*hypoconulid*) of Osborn's talon. This hypoconulid is in fact the real "talon," viz. that part which is so generally well developed on the posterior side of third lower molars, but which in many Sciuromorpha can be distinctly made out in the anterior molars too, as well as in milk-teeth of *Lepus* and *Myolagus*, and both in milk-teeth and permanent molars of *Lagodus* and *Titanomys*[4].

The conclusions to be drawn from the foregoing analysis are, I am glad to state, the very same at which Scott has arrived, as they tend to show, even more unmistakably, "that the Rodents are to be derived from the same generalized group of primitive placental Mammals, the Bunotheria, to which we refer the origin of the Ungulates, Creodonts, and Lemuroids"[5]. In respect to what Scott considers plainly to be "the tuberculer pattern" of superior molars, it cannot be denied that there appear three principal cusps, two external and one internal one, in the upper molars of *Plesiarctomys sciuroides*; but there are other parts to be seen, even in these much-worn molars, and I have already pointed out that it is dangerous to draw inferences from *worn* teeth.

Very similar remarks apply to two papers by Schlosser[6], in which this author endeavours to refer the molars of Rodentia to trituberculism. I therefore refrain from discussing them at length, and I wish only to remark upon the second of the papers quoted. Schlosser asserts in the most positive manner, what at first sight appears to be a startling fact, that *Plesiadapis* and *Protoadapis*, from the Lower Eocene of Reims, are Rodentia. *Plesiadapis* had previously been

[1] *Cf., e. g.*, H. F. Osborn and J. L. Wortman, "Fossil Mammals of the Wahsatch and Wind River Beds." Collection of 1891. *L. c.* p. 86, figs. 1 & 2.

[2] *Ib.*

[3] *L. c.* p. 476, and pl. xi. fig. 1 *d*.

[4] See also the inferior molars of "*Plesiadapis*" in Lemoine, "Etude d'ensemble sur les dents des Mammifères fossiles des environs de Reims" (Bull. Soc. Géol. de France, trois. série, t. xix. Mai 1891, pl. x. fig. 65 *e*), and of *Dectiadapis*, ibid. pl. xi. fig. 146 *e*, 146 *ss*.

[5] Scott, *l. c.* p. 478.

[6] Max Schlosser, "Die Differenzirung des Säugethiergebisses" (Biol. Centralblatt, Band x. Nos. 8 & 9, Erlangen, 1 & 15 June 1890, pp. 250, 251).—*Id.*, "Ueber die systematische Stellung der Gattungen *Plesiadapis*, *Protoadapis*, *Pleuraspidotherium* und *Orthaspidotherium*" (Neues Jahrb. f. Mineralogie, Geologie und Paläontologie, Jahrgang 1892, Band ii. pp. 239, 240).

considered by Schlosser himself to be a Lemurid[1], and Osborn[2] had placed both of them amongst the Pseudolemuridæ. Whilst fully agreeing with Schlosser in his main conclusions, for reasons which I shall discuss elsewhere, I am again at a loss to see what tuberculism has to do with the matter[3], and would put but one question: How comes it that both *Protoadapis* and *Plesiadapis*, which are indeed the most ancient types of Rodents hitherto known, show the so-called heel of inferior molars in such a perfect condition[4] in spite of tuberculism, which considers these parts as a late addition to the original triangle of inferior molars?

I have declared myself opposed to the tubercular theory, but have limited my remarks hitherto merely to criticism, though occasionally I offered some positive argument in favour of an hypothesis which is in many points the very reverse of the prevailing theory. It remains now for me to justify the position I have taken with regard to it; what I am going to say is partly a summing up of preceding remarks, and partly embraces a far wider field, and will, I have no doubt, meet with some opposition.

No better starting-point could be chosen than the "*Sciuridæ*," amongst which we meet with the most primitive form of molars of this low order of Mammalia.

The adherents of tuberculism assert that they have proved the Mammalian molar to be traced back to a more and more simple form. I have tried to show that they have failed to do so, and in my turn assert that the molar of Placentalia can be traced to a polybunous form, and that the real tubercular pattern is a more specialized secondary stage. So that, as a matter of course, the cardinal point to be established is to show, that the more complex forms, which in the Lower Eocene as well as in the recent period are found side by side with the simpler forms, tuberculate or otherwise, are indeed the primitive, the more generalized type.

To prove my assertion, I start from five assumptions:—

1. *Brachydonty is the more primitive, the more generalized condition of molar form, and so is*
2. *Bunodonty, as opposed to Lophodonty (or Zygodonty, which is the same thing).*
3. *The more brachydont a molar is, the more multituberculer it is, or, let us say, polybunous.*
4. *The transformation, viz., the reduction and simplification, pro-*

[1] M. Schlosser, "Die Affen, Lemuren, Chiropteren, Insectivoren etc. des europäischen Tertiärs, etc." Pt. I. Wien, 1887, p. 47.

[2] Henry Fairfield Osborn, "A Review of the Cernaysian Mammalia" (Proc. Phil. Acad. Nat. Sci., May 6th, 1890, pp. 55, 56).

[3] "Dass aber dieser Typus (*i. e.* Tuberculartypus) auch den Ausgangspunkt für die oberen Molaren der Nager darstellt, ersehen wir daraus, dass er sich bei *Sciurus* sogar noch bis in die Gegenwart ziemlich rein erhalten hat." (*L. c.* p. 240.)

[4] Lemoine, *l. c.* pl. x.

ceeds from the inner side outwards in superior, and from the outer side inwards in inferior molars.

5. *The now prevalent transverse arrangement of cusps or lobes is not the primitive condition, but a specialized pattern of the crown.*

The first two points need no discussion, as no biologist of the present day denies them. I thirdly maintain that *the more brachydont a molar is, the more polybunous it is*; so that change, which in our case means reduction, simplification, of the molar-crown elements, goes hand in hand with the gradual progress from brachydonty towards hypsodonty.

In the general survey of Sciurine teeth, it has already been shown that the more the molars are brachydont, the more they are polybunous, so that by this statement alone polybuny is proved to be the primitive condition.

If we examine the outer parts of upper and the inner parts of lower molars, we see that they present much less variation in Brachydontia as compared to Hypsodontia, and in the various stages of Hypsodontia compared together, than does the rest of the crown, especially the inner side in upper and the outer side in lower molars. It therefore at once strikes us, that the outer side of upper and the inner side of lower molars (viz., those parts which, when the jaws are at rest, are protruding over the corresponding parts of the opposite jaw) have undergone the least modifications, that they are the more stable elements of molars. These same sides being generally more complex than the *inner* side above and the *outer* below, we may infer from it that the complex condition is the primary one, and that the reduced, simplified state of the inner side above and the outer side below is a specialized condition, the beginning of which we see already in molars of *Cretaceous Mammalia* and in those of *Ornithorhynchus*.

The extreme of this specialized condition is what has been called trituberculism, and considered to be a primitive pattern of Eutherian molars. It is not more primitive in Ungulata, Condylarthra, Creodonta, and Lemuroidea than in *Sciurinæ*, the species of which, when there is only one cusp on the inner side of upper molars, present an approach to trituberculism.

Now, what is the meaning of this reduction on the inner side of superior, and the outer side of inferior molars?

We have seen that in perfectly brachydont teeth the outer and inner sides of the molars present the least difference from each other in longitudinal extension, as well as in the number of their cusps; and that the superior molar becomes shortened on its inner side, as well as the inferior on its outer side, by the excessive development of some cusps (generally either one or three, rarely two, in *Sciurinæ*) at the expense of others, which are present in such perfectly brachydont teeth as those of *Eosciuri* or *Rhithrosciurus*. The meaning of this process of reduction becomes obvious, when we consider that the internal cusps of superior,

and the external cusps of inferior, molars have to fit into the hollows or valleys of the opposing teeth. When there is only one cusp exclusively or prominently developed on the inner side of a superior molar, as in the so-called tritubercular, or at a lesser degree in the trigonodont type, this single cusp fits in the more or less cup-like depression of the posterior moiety of the corresponding inferior molar; in other words, the *protocone*,—viz., the oldest element of upper molars, according to the tritubercular theory—fits in what the theorists consider to be the most modern part of inferior molars. And, *vice versa*, the *postero-external* cusp of inferior molars, that is the *hypoconid* of the "heel," has to fit in the median valley of superior molars, formed essentially by the three cusps of what trituberculism considers to be the primitive trigon of upper molars.

The special development of two inner cusps in superior molars has been shown to be so very rare an occurrence in *Sciurinæ*, that up to the present day it was known only in some fossil forms (*Sciuroides*, *Pseudosciurus*, *Ischyromys*), whereas it is the predominant feature amongst Ungulata. To these two inner cusps correspond two hollows or valleys of the inferior tooth. The relative development of the anterior valley, formed by the so-called primitive trigon of inferior molars, corresponds to that of the postero-internal cusp of superior molars,—the *hypocone*, a later addition according to the tritubercular theory: when the hypocone is suppressed, as in the pure tritubercular type, or feebly developed, as in the trigonodont type, the anterior valley in the lower molars is atrophied or insignificant. It is well developed, to receive the hypocone as a pestle, when this last has the same or almost the same size as the protocone.

Fourthly, we are able to state that *the transformation, viz. the reduction and simplification, proceeds from the inner side outwards in superior, and from the outer side inwards in inferior molars.* Here I have to repeat what I said with regard to semi-hypsodont teeth, viz., that the vertical elevation of the crown, the first stage towards hypsodonty, always has its starting-point from the *inner* side of upper molars. A farther stage of semi-hypsodontism, as presented by the rooted molars of Miocene *Lagomorpha* (*Lagodus*), shows how hypsodontism gradually extends towards the outer side, accompanied by a gradual and essential change of the pattern of the crown. In the same way the inner root, which ultimately will remain open, gradually extends outwards, increasing in size, and receives a coating of enamel. This process is so slow, that for a long time the outer side retains a brachydont as well as a complex conformation.

The fifth point advanced was stated as follows:—*The now prevalent transverse arrangement of cusps or lobes is not the primitive condition, but a specialized pattern of the crown.* What, then, was the primitive condition? The primitive generalized pattern was the exact reverse, viz., the arrangement of cusps in longitudinal series, separated by longitudinal grooves or valleys. This is, indeed,

a cardinal point and will, when once generally recognized, appear to be a simple truth.

Bunodonty, as opposed to lophodonty, is the first step from a transverse arrangement towards the longitudinal one, and is not always to be distinguished at once from the second step I am speaking of, though this last is often characterized by a sort of asymmetry, or confusion, in a way, as is usually the case in transitional stages.

First, as to *Sciurinæ*. As has already been said, transverse *crests* are to be found only in semi-hypsodont types, many of which tend towards the Hystricomorpha, which for their lack of brachydont molars at once show themselves to be more specialized forms. With the exception of Myoxine types—and this exception is only an apparent one—we may say that the more the molars tend towards brachydonty, the more the crests are broken up into cusps. Of these cusps there are generally five on the outer side of upper molars, two or three of which have been prominently developed. In the middle two intermediate, and on the inner side in the same manner as on the other side, originally a *longitudinal* series of cusps were developed, which very soon, viz., when the tooth ceases to be perfectly brachydont (as well as in somewhat worn semi-hypsodont or hypsodont teeth), are reduced in number and tend to become coalesced, a middle *cusp* appearing the most developed. This middle cusp seems to be for the greater part the remnant of a fifth series which have become partially atrophied, in order to give place for the median transverse valley; and it is in consequence of the formation of this valley that the cusps appear arranged in transverse series, even before being connected as ridges or crests.

In superior and inferior molars, the most brachydont members of the family are at the same time those which show a tendency towards a longitudinal alignment of their cusps. The difference between superior and inferior molars consisting in the presence in upper molars of intermediate cusps, in more specialized, viz. less brachydont forms, generally reduced to two, as before stated, but which, as shown by the most brachydont forms, are the remnants of one or more longitudinal series of cusps or tubercles, intermediate between the outer and the inner series.

The cup- or basin-like shape of inferior Sciuromorphine molars is but a slight specialization of a primitive type, a disposition of the cusps on the outer and inner margin, with an intervening longitudinal depression. The slight specialization consists in the beginning of a transverse arrangement. In the Bornean *Rhithrosciurus* (Plate IX. fig. 2), the whole of the very brachydont inferior molars consists mainly of two series of marginal cusps, none specially developed, and with a spacious longitudinal groove dividing the outer from the inner series; thus pointing significantly towards some primitive mammalian molars remote in time (*Microlestes*). And so the curious *Pseudosciurus*, from the Upper Eocene of Southern Germany, shows the tendency towards, or, as we rathe

should say, the traces of, a primitive arrangement of its tubercles of upper molars in three longitudinal series, there being two rows in the lower molars.

This paper does not pretend to enter into details as to other families and orders. But I think it important to state in a few words that this tendency of older forms towards a longitudinal arrangement is quite general in Rodents as well as in Creodonts, Lemuroids, and Ungulates. In Sciuridæ we have very primitive forms still existing side by side with those more specialized, so that the transverse arrangement does not at first sight appear to be a later transformation. The Lagomorpha are in this respect, as in others, highly instructive, the molars of the living members being very specialized. I hope to show fully on another occasion that the structure of the molar form of Lagomorpha is to be traced back from the perfect transverse direction presented by their enamel-ridges to a polycodoid type of molar, that means, to a molar approaching closely to those of *Polycodus*, a mammal from the Lower Eocene of North America and Egerkingen in Switzerland, which has hitherto been considered to be a Lemuroid. In a somewhat lesser degree, the Lagomorphan molar tends towards *Esthonyx*, considered by Cope [1] to be one of the progenitors of Rodentia.

The intermediate stages are the unworn milk-teeth, premolars and molars, of young *Lepus*, the Miocene *Paleolagus*, *Lagomys*, the Pleistocene, Pliocene, and Miocene *Myolagus*, and the Miocene *Lagodus*. The anterior upper and lower premolar of *Lepus*, the second superior and the anterior inferior premolar of *Lagomys*, the superior premolars and more or less all the superior molars of *Myolagus*, as well as the inferior anterior premolar of the latter, show, even in adult specimens, a conformation which points unmistakably towards a longitudinal arrangement of partially sharp-edged cusps—these cusps being three longitudinal series separated by two longitudinal grooves in the upper teeth, and two series with one intermediate longitudinal groove in the lower molars. The difference between the first lower premolar and the other grinding-teeth is very striking, especially in *Myolagus*, for which I refer to a figure from Filhol's memoir on the Sansan fauna [2].

As to other Orders, I must be satisfied to give a few instances. Amongst recent Carnivora, the Subursi, especially *Ailurus*, and partially the Ursidæ themselves, show unmistakably the longitudinal arrangement of their molar cusps. In the same direction the milk-teeth of several Orders point significantly, even those of modern Ruminants.

In the Lower Eocene many molars of various Orders tell the same tale as to their origin, often in a distinct manner. In favour of my view I refer to the following figures:—First, from Cope's

[1] E. D. Cope, "The Mechanical Causes of the Development of the Hard Parts of the Mammalia" (Journal of Morphology, vol. iii. Boston, U.S.A. 1889, p. 263).

[2] 'Etudes sur les Mammifères fossiles de Sansan' (Paris, 1891), pl. i. fig. 8.

Tertiary Vertebrata: *Calamodon*[1], *Anisonchus*[2], *Ectocium*[3], *Peripty-chus carinidens*[4], *ditrigonus*[5], and *rhabdodon*[6], *Palæosyops lævidens*[7], *Phenacodus*[8], *Protogonia*[9]. Secondly, from Lemoine's 'Etude d'ensemble sur les dents des Mammifères des environs de Reims'[10]: *Hyænodictis*[11], *Dissacus*[12], *Arctocyon*[13], *Lophiodochœrus*[14], *Pleura-spidotherium*[15], *Pachynolophus maldani*[16], *Protodichobune owenii*[17]. Thirdly, from Rütimeyer's 'Eocäne Säugethierwelt von Eger-kingen'[18]: *Ailuravus*[19], *Pelycodus helveticus*[20], *Hyopsodus*[21], "*Plesi-adapis*?"[22], *Acotherulum*[23], *Cebochœrus*[24], *Lophiodon parisiense*[25], *Paloplotherium magnum*[26]; the last two only so far as their milk-teeth are concerned.

I wish to answer in advance an objection which will certainly have occurred to the reader. The extreme of complication is met with in such highly specialized recent forms as *Hydrochœrus*, *Phacochœrus*, and *Elephas*, and to a lesser extent in semi-rooted molars, especially amongst Rodentia. As to the supposed more complex form of these last, it is only apparent. A worn molar of *Hystrix*, for instance, seems rather more complex than the rooted molar of *Erethizon*, but on examining unworn grinding-teeth of *Hystrix*, even the seemingly very complex milk-tooth only presents five more or less transverse enamel-folds.

The worn molars show a large quantity of enamel-islets, and thus have a very complex appearance; but this is not the consequence of an augmentation of enamel substance, or additional cusps, but, on the contrary, of diminution of the enamel, which diminishes in the proportion that the worn surfaces approach the roots.

Besides, I have always maintained that in progress of time a new addition may occasionally have occurred in molars; but it would appear that in one instance at least I was mistaken. Contrary to Owen[27], and all later palæontologists, with the only

[1] 'The Vertebrata of the Tertiary Formations of the West,' pl. xxiv. e. fig. 22.
[2] *L. c.* pl. xxiv. g. fig. 6.
[3] *L. c.* pl. xxv. e. fig. 12.
[4] *L. c.* pl xxiii. d. figs. 14, 15, pl. xxiv. g. fig. 5.
[5] *L. c.* pl. xxiii. g. fig. 12, pl. xxix. d. fig. 2–4.
[6] *L. c.* pl. lvi. f. figs. 1 *a*, 2 *a*.
[7] *L. c.* pl. l. fig. 3.
[8] *L. c.* lvii. b. fig. 1.
[9] *L. c.* pl. xxv. e. fig. 13, pl. xxix. f. fig. 1 *a*, pl. lvii. f. fig. 8.
[10] *L. s. c.*
[11] *L. c.* pl. x. fig. 4.
[12] *L. c.* pl. x. fig. 2.
[13] *L. c.* pl. x. figs. 14, 18, 20, 22, &c.
[14] *L. c.* pl. xi. fig. 129.
[15] *L. c.* pl. xi. fig. 87.
[16] *L. c.* pl. xi. figs. 117, 118.
[17] *L. c.* pl. xi. fig. 132.
[18] *L. s. c.*
[19] *L. c.* pl. vii. figs. 18, 19.
[20] *L. c.* pl. viii. fig. 1 (partim).
[21] *L. c.* pl. viii. figs. 7, 8.
[22] *L. c.* pl. viii. figs. 16, 17, 21.
[23] *L. c.* pl. iv. figs. 22, 24.
[24] *L. c.* pl. iv. fig. 30.
[25] *L. c.* pl. i. fig. 8 (d_3 sup.).
[26] *L. c.* pl. i. fig. 1 (*d* sup.).
[27] Rich. Owen, "Description of the Cavern of Brumiquel and its Organic Contents. Part II. Equine remains" (Phil. Trans. vol. 159, London, 1870, p. 537).

exception of Kowalevsky, who, in the same 22nd volume of the 'Palæontographica,' had expressed an identical view, I had supposed that the two inner lobes of upper equine molars are not homologous with those of *Anchitherium*, but are a more modern addition to the tooth. Now ontogeny, according to Klever [1], suggests that Kowalevsky and myself are wrong.

As to the molars of *Hydrochœrus*, *Phacochœrus*, and *Elephas*, I leave them to ontogenists; and, if I am not mistaken, there is every appearance that we shall not have to wait very long for an answer.

It may be asked whether the pattern of molars towards which the types of almost all the Orders of Mammalia represented in the Lower Eocene tend is nowhere realized.

When I first saw the plates of Marsh's "Discovery of Cretaceous Mammalia," my impression was that the molars figured on plate ii.[2] constitute one of the most important discoveries as regards the ancestry of Placentalia, inasmuch as these figures correspond to what I considered, and have been expounding just now, to approach the presumed *ancestral* form of Mammalian molars. In going over the text, I found that Marsh collocates all these multituberculars teeth in the "aberrant" Order of Allotheria, and states expressly, that "Carnivores, Rodents, and Ungulates appear to be entirely wanting in this unique fauna," and that "a still more surprising fact is the absence of their probable ancestors, unless, indeed, the insectivorous forms are entitled to this important position: many known facts point in this direction" [3]. In Part III. of "Discovery of Cretaceous Mammalia" Marsh again states: "These remains are not transitional between Mesozoic and Tertiary forms, but their affinities are with the former beyond a doubt" [4].

To me it appears, from what we now know of those important fossils called *Allotheria*, we are not entitled to consider the whole Order as an aberrant one, though there may be, and certainly are, aberrant genera. But, on the whole, the Allotheria are not more aberrant than the Myomorpha, for instance.

The discovery of the Laramie mammals led to a controversy between their discoverer and another eminent American palæontologist; but this side of the question has not been taken into consideration, both disputants being agreed in assuming that the multitubercular teeth in question belong to an aberrant group. This aprioristic assumption may have prejudiced the impartial investigation of facts. I cannot enter fully into the question, especially as it would be rash to pronounce too positively on an

[1] Ernst Klever, "Zur Kenntniss der Morphogenese des Equidengebisses" (Morphol. Jahrb. xv. 1889, Leipzig, pls. xi.–xiii.).

[2] O. C. Marsh, "Discovery of Cretaceous Mammalia," American Journal of Science, vol. xxxviii. July 1889, plate ii.

[3] *L. c.* p. 83.

[4] "Discovery of Cretaceous Mammalia.—Part III.," *l. c.* vol. xlii. March 1892, p. 250.

examination of the figures and descriptions without having seen the originals; but I wish to offer a few remarks.

Marsh has considered a certain number of isolated molars, possessing three longitudinal pairs of elevations, to be upper molars, although the type of *Dipriodon robustus*, the only molar which is *undoubtedly* from the upper jaw, left side, "its position being decided by a portion of the maxillary attached to it,"[1] apparently has only two longitudinal rows. This circumstance has given origin to part of Osborn's criticisms[2]. The type of *Tripriodon cœlatus*[3], considered by Marsh[4] as the first upper molar of the left side, as well as the type of *Selenacodon fragilis*[5], also stated to be an upper molar (both having three longitudinal rows of cusps), are declared by Osborn to be respectively a last lower molar of *Meniscoessus*, and an anterior lower molar of the same[6]. In a subsequent note[7] Osborn writes as follows:—"It remains for the author to show specifically that the types of *Selenacodon* and *Tripriodon* are maxillary teeth," adding: "I should myself have considered them as such but for the fact that the type of *Dipriodon robustus*, with two rows of tubercles, was described as a maxillary tooth, and figured with a supposed fragment of the zygomatic arch attached to the alveolar border." With regard to the upper molars, Marsh asserts, in his latest paper on the subject, that he has the means of showing what Osborn has objected to: "Although not found in position in any one specimen, so many have been secured with portions of the jaw attached, that their place in the dental series has been ascertained in several forms;" and he goes on to state, "that the upper molar teeth may be separated into two series, the first having three longitudinal rows of elevations on the crown, and the second series but two rows"[8]. With the caution imposed by the fact that I am judging only from the published figures, I venture to suggest that the type of *Dipriodon robustus*, which has the undoubted fragment of the zygomatic arch attached to the alveolar border, had originally three longitudinal rows of cusps, the middle one being worn off. Marsh himself states that its "points are somewhat worn"[9], and this appears to me clearly shown in his figure[10]. If we now assume that where there are three rows of tubercles above and two below, "the cusps of the lower rows fit into the valleys of the upper teeth"[11] (which in my

[1] Marsh, *l. c.* part I. p. 85, pl. ii. figs. 13–15.

[2] As stated by Osborn himself in "A Reply to Professor O. C. Marsh's 'Note on Mesozoic Mammalia.'" Reprinted with slight alterations from the 'American Naturalist,' September 1891, p. 782.

[3] Marsh, *l. c.* part I. pl. ii. figs. 19–21.

[4] *L. c.* p. 86.

[5] Marsh, *l. c.* part I. pl. ii. figs. 22–24, p. 86.

[6] H. Fairfield Osborn, "A Review of the Cretaceous Mammalia" (Proc. Acad. Nat. Sc. Philadelphia, 1891, p. 128).

[7] A Reply to Professor O. C. Marsh's Note, &c., p. 782.

[8] Part III. p. 253.

[9] Part I. p. 85.

[10] *L. c.* pl. ii. figs. 13, 14.

[11] Osborn, "A Review of the Cretaceous Mammalia."

opinion allows only for a movement in the longitudinal direction), this mechanical action of the jaw would be followed by the wearing away first of all of the middle row of the upper molars, which rubs against the inner and outer side respectively of the outer and inner row of the opposing tooth. Compared with the types of "*Tripriodon cœlatus*"[1] and "*caperatus*"[2], *Dipriodon robustus* shows its inner cusps unproportionally extending outwards, and this would justify the supposition that the remnants of two cusps of the middle row have united with what remains of the enamel-folds of the two inner cusps, a mode of coalescence which we often see realized in worn molars. I therefore fail to find in Marsh's previous publications the proofs of the statement made by him[3] that one series of upper molar teeth of Cretaceous Allotheria has but two rows; although from certain analogies—with the molars of *Mus* on the one side, those of *Cricetodon* on the other—analogies which may hereafter turn out to be homologies, I am quite willing to admit that Prof. Marsh may have in his hands the means for proving it. I cannot admit Osborn to have satisfactorily shown that in this group of Cretaceous Allotheria there are lower molars with three rows of cusps. If there were three rows of cusps with two longitudinal grooves in the lower molars, we would have to urge four rows of cusps with three longitudinal grooves in the upper molars; these have not been forthcoming up to the present date. Thus there seems to be no reason for denying Marsh's statement that "the lower molars . . . . although differing widely in the form and structure of their crowns, have only two parallel series of crescents or tubercles, an outer and inner row, with a groove or valley between them"[4].

For my present purpose it may be sufficient to point out, that both authors agree in stating that there are several forms with upper molars composed of three longitudinal rows of cusps with two grooves between them, to which correspond two longitudinal rows with one groove in the lower molars; but, as stated before, they have not furnished sufficient proof for their opinion that these molars belong to an aberrant Order of Mammalia. In comparing the teeth in question with those of the Muridæ and more particularly of *Mus*, it becomes evident that the main differences between them consist in this, that whilst in the Cretaceous molars the prevailing division is effected by longitudinal grooves, in *Mus*, on the contrary, the molars are deeply divided by transverse grooves: the longitudinal grooves in this genus, of which there are two in the upper, and one in the lower molars, being relatively shallow. For further particulars on this argument, as far as it relates to Muridæ, I refer the reader to a paper by Hensel on *Mus orthodon* from the Ossiferous Breccias

[1] *L. c.* part I. pl. ii. figs. 19, 20.
[2] *L. c.* part III. pl. v. fig. 2.
[3] *L. c.* part III. p. 253.
[4] *Ib.* p. 253.

of Sardinia[1], and to a subsequent paper by myself on the same subject[2].

Marsh has recently made the following statement:—"One fact is becoming more and more evident, the near affinity of the early Primates, Carnivores, Ungulates, and Rodents, with each other and with the Insectivores, and more remotely with Marsupials. The key to the mystery lies concealed in the great break between the Lower Wahsatch, at the base of the Eocene as now known, and the Laramie beds of the Cretaceous. In the latter, none of the above placental mammals have been found, but in the early Eocene occur, side by side, Carnivores, Rodents, and Ungulates ..."[3]

I have endeavoured to show that the key to the mystery actually lies for the chief part in Prof. Marsh's own hand, and I trust that he himself will before long furnish us with the full proofs that several at least of the Cretaceous Allotheria, so called, are in the direct ancestral line of Eutheria.

And, in the meanwhile, I confidently state as follows my conclusions as to the primitive type of the Eutherian molar:—

(1) The primitive condition of the Eutherian molar is that of polybuny.

(2) The single tubercles or cusps were arranged in longitudinal series (*Tinotaxis*), divided by longitudinal grooves or valleys, there being generally three rows with two grooves in the upper, and two rows with one groove in the lower molars.

(3) *Microlestes* may prove to be a remote ancestor of the Eutheria.

[1] R. Hensel, "Beiträge zur Kenntniss fossiler Säugethiere.—II. Ueberreste von *Mus* in der Breccie von Cagliari," Zeitschr. d. deutsch. geolog. Gesellschaft, viii. Band, 1856, p. 281. The conformation of the first upper molar of *Mus* is described by Hensel as follows:—"Seine Krone zerfällt durch zwei fast bis auf den Grund der Krone eindringende Querfurchen in drei Querleisten, von welchen die beiden ersten nach vorn convex, nach hinten zu concav erscheinen ... Zwei verhältnissmässig seichte Längsfurchen zertheilen wiederum jede Querleiste in drei mehr oder weniger deutliche Höcker ... Das Schema für die Backenzähne des Unterkiefers (Fig. 11*b*) ist ein wesentlich anderes. Zwar sind auch hier die Kronen durch zwei Querfurchen in drei Querleisten getheilt. Allein statt zweier Längsfurchen findet sich nur eine, so dass jede Querleiste in zwei Höcker, die ganze Zahnkrone also in sechs derselben zerfällt." (*L. c.* p. 282.)

[2] Forsyth Major, "Sulla conformazione dei Molari nel Genere *Mus*, e sul *Mus meridionalis* e *Mus orthodon*, Hensel," Atti Soc. Tosc. Sc. Nat. Proc. Verb. 1888, pp. 129–145.—Mr. Oldfield Thomas has lately drawn my attention to his "Description of a new Genus and Species of Rat from New Guinea," the *Chiruromys forbesi* (Proc. Zool. Soc., April 17, 1888, pp. 237–240, fig. 2, p. 239). In this paper it is stated that the teeth of *Chiruromys* "are remarkably complicated, and show a high degree of specialization, far more than is found in any other genus at all allied to the present one," and that "this extreme specialization both of teeth and tail is especially remarkable in an animal inhabiting such a refuge for old and little-modified forms as New Guinea." From what I have been saying, it is to be inferred, that the teeth in question, far from showing a high degree of specialization, are, on the contrary, of a very generalized type, precisely such as we might anticipate to meet with in a refuge for old and little-modified forms.

[3] O. C. Marsh, "A new Order of extinct Eocene Mammals (Mesodactyla)," in American Journal of Science, vol. xlii. May, 1892, p. 449.

(4) From the polybunous molar, as characterized before, have been derived the other types of Placental molars, by a gradual transformation of the longitudinal arrangement of cusps into a transverse one (*Chiastotaxis*), and by a prevailing development of a few cusps—a sort of Oligarchy—as well as by the fusion and suppression of others, several of which are, however, maintained with great persistency in a secondary condition.

(5) In the upper molars two outer cusps and one or two inner cusps are usually the most developed.

(6) The truly tritubercular molar is but a very specialized stage, which is often preceded, *not followed*, by Rütimeyer's trigonodont type.

(7) The supposition that the so-called *heel* or *talon* of inferior molars is a later development, is an arbitrary one, disproved by facts.

(8) Which of all the cusps of the primitive polybunous molar or its derivatives may be "homologous with the reptilian cone," I do not know.

VI. EXPLANATION OF THE PLATES.

Plate VIII.

Right superior molars, much magnified, of:—

Fig. 1. *Sciurus* (*Eosciurus*) *indicus*, Erxl. m_1. (B.M. 1203 *a*.)
2. *Sc. prevosti*, Desm. m_1. (B.M. 5836.)
3. *Sc. lokroides*, Hodgs. m_1. (B.M. 1868/4 . 4.3.)
4. *Sc. everetti*, Thos. m_2. (B.M. 1892/9 . 6.8.)
5. *Xerus* (*Exerus*) *hosei*, Thos. p_1. (B.M. 1892/7 . 19.2.)
6. *Xerus* (*Exerus*) *insignis*, Fr. Cuv. m_1. (B.M. 68 *c*.)
7. *Xerus* (*Protoxerus*) *stangeri*, Waterh. m_1. (B.M. 515 C.)
8. *Xerus* (*Protoxerus*) *aubinnii*, Gr. m_1. (B.M. 1875/4 . 30.4.)
9. *Xerus* (*Atlantoxerus*) *getulus*, Gesn. m_2.
10. *Xerus erythopus*, Geoff. m_2. (B.M. 1888/11 . 4.4.)
11. *Xerus* (*Exerus*) *laticaudatus*, Gr. m_1. (B.M. 1885/8 . 1.272.)
12. „ „ p_1. „
13. *Anomalurus fraseri*, Waterh. p_1. (B.M. 555 *c*.)
14. *Anomalurus beecrofti*, Fras. m_1. (B.M. 1066 *b*. 1886/1 . 5.1.)
15. *Xerus* (*Paraxerus*) *pyrropus*, Fr. Cuv. m_1. (B.M. 897 *a*.)
16. *Xerus* (*Exerus*) *berdmorei*, Bly. (juv.) m_1. (B.M. 1878/6 . 17.51.)
17. „ „ (middle age). m_1. (B.M. 1878/6 . 17.33.)
18. „ „ (old). m_1. (B.M. 1861/4 . 12.13.)
19. *Pteromys leucogenys*, Temm. m_1. (B.M. 556 *b*.)
20. *Sciuropterus pearsoni*, Gr. m_2. (B.M. 1883 *a*.)
21. *Sciuropterus horsfieldi*, Waterh., type. m_1. (B.M. 1855/12 . 24.102.)
22. *Xerus* (*Paraxerus*) *cepapi*, Smith. m_1. (B.M. 1885/12 . 8.2.)
23. *Xerus* (*Paraxerus*) *pyrropus anerythrus*, Thos. m_1. (B.M. 1890/6. 8.22.)
24. *Xerus* (*Paraxerus*) *isabella*, Gr. m_2. (B.M. 1862/5 . 9.3.) Cameroons.

Plate IX.

Right inferior molars, much magnified, of:—

Fig. 1. *Sciurus* (*Eosciurus*) *indicus*, Erxl. m_1.
2. *Rhithrosciurus macrotis*, Gr. m_1. (B.M. 1888/8 . 13.7.)
3. *Sciurus lokroides*, Hodgs. m_1.
4. *Sciurus everetti*, Thos. m_2.

Fig. 5. *Xerus* (*Eoxerus*) *hosei*, Thos. p_1.
6. *Xerus* (*Eoxerus*) *insignis*, Fr. Cuv. m_1.
7. *Xerus* (*Protoxerus*) *stangeri*, Waterh. m_1.
8. *Xerus* (*Protoxerus*) *aubinnii*, Gr. m_1.
9. *Xerus* (*Atlantoxerus*) *getulus*, Gesn. m_2.
10. *Xerus erythopus*, Geoff. m_2.
11. *Xerus* (*Eoxerus*) *laticaudatus*, Gr. p_1.
12. ,, ,, m_1.
13. *Anomalurus fraseri*, Waterh. p_1.
14. *Anomalurus beecrofti*, Fras. m_1.
15. *Xerus* (*Paraxerus*) *pyrropus*, Fr. Cuv. m_1.
16. *Xerus* (*Eoxerus*) *berdmorei*, Bly., juv. m_1.
17. ,, ,, middle age. m_1.
18. ,, ,, old. m_1.
19. *Pteromys leucogenys*, Temm. m_1.
20. *Sciuropterus pearsoni*, Gr. m_2.
21. *Sciuropterus horsfieldi*, Waterh., type. m_1.
22. *Xerus* (*Paraxerus*) *pyrropus anerythrus*, Thos. m_1.
23. *Xerus* (*Paraxerus*) *cepapi*, Smith. m_1.
24. *Xerus* (*Paraxerus*) *isabella*, Gr. m_2.

Plate X.

Fig. 1. *Sciuropterus albanensis*, n. sp. (Middle Miocene of Grive-Saint-Alban.) Upper incisor. *a*, from the outer, *b*, from the inner, *c*, from the anterior side.
2. *Xerus* (*Eoxerus*) *grivensis*, n. sp. (Middle Miocene of Grive-Saint-Alban.) Left mandibular ramus, nat size.
3. m_1, m_2, m_3, of the same; magn. $\frac{6}{1}$.
4. *Sciurus spermophilinus*, Dep. p_1, m_1, m_2 sup. sin.; magn. $\frac{6}{1}$.
5. ,, ,, Anterior view of inf. incisor; magn.
6. ,, ,, Left mandibular ramus, inner view, nat. size.
7. ,, ,, Left mandibular ramus, outer view, nat. size.
8. ,, ,, p_1, m_1, m_2, m_3, inf. sin., upper view; magn. $\frac{6}{1}$.
9. ,, ,, The same as fig. 8, inner view; magn. $\frac{6}{1}$.
10. *Nannosciurus concinnus*, Thos. (Isabella, Basilan, Philippines), type. (B.M. 1940 *a*. 1876/10.4.7.) d_1, m_1, m_2, m_3, inf. sin.; magn. $\frac{6}{1}$.

Plate XI.

Fig. 1. *Sciuropterus tephromelas*, Günth. Malay Peninsula. (B.M. 1885/8.1.126.) Left mandibular ramus. Nat. size. From the inner side.
2. The same. m_2; magn. $\frac{3}{1}$.
3. *Sciuropterus albanensis*, n. sp. (Middle Miocene of Grive-Saint-Alban.) Left mandibular ramus, from the inner side; nat. size.
4. The same from the outer side; nat. size.
5. The grinding-teeth of the same, upper view; magn. $\frac{5}{1}$.
6. *Nannosciurus minutus*, Du Chaillu. W. Africa. (B.M. 1794 *a*. 1861/7.29.19.) Superior grinding-teeth of the right side (p_1, m_1, m_2, m_3); magn. $\frac{6}{1}$.
7. *Nannosciurus concinnus*, Thos., juv. Superior grinding-teeth of the right side (d_1, m_1, m_2, m_3); magn. $\frac{6}{1}$.

2. Observations on the Development of the Rostrum in the Cetacean Genus *Mesoplodon*, with Remarks on some of the Species. By Henry O. Forbes, F.Z.S., F.R.G.S.

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(Plates XII.–XV.)

In the course of my duties as Curator of the Canterbury Museum, Christchurch, N. Z., I had occasion to study the Cetacea in that collection. In my determination of the species of *Mesoplodon* I was necessarily guided by the authoritative papers on this group by Sir William Flower in the 'Transactions' of this Society, and by Sir William Turner in his Report on the Cetacea of the 'Challenger' Expedition. In his paper in volume x. of our 'Transactions,' page 422, Sir William Flower observes, in speaking of a form near to *Mesoplodon grayi*, Haast:—"Making every allowance for individual variation, it scarcely seems possible that a rostrum such as that shown in figure 2 [i. e. *Mesoplodon grayi*: Plate XIV. fig. 3] could change in the course of growth to that in figure 3 [i. e. *Mesoplodon haasti*, Flower: Plate XII. fig. 2]. If so, most of the determinations of the fossil species based solely on the form of the rostrum are quite valueless." The same author, on an earlier page (page 420) of the same paper, remarks:—"There is still much to be learned with regard to the mode of ossification of this cartilage. All the specimens which I have had an opportunity of examining are either so young that ossification has not commenced, and the trough of the vomer in the rostrum proper is completely empty in the dried skull, or so old that the consolidation of the cartilage and its union with the surrounding bone has been completed." In having lived for some time in the region in which this genus is not uncommon, I have been fortunate in having had an opportunity of examining several immature crania in which the relations of the bones which constitute the rostrum were such as to enable me to trace some unobserved stages in their development. These observations I have thought of sufficient interest to lay before the Society, especially as they bear on some of the characters by which the various forms of *Mesoplodon* and *Ziphius*, both recent and fossil, have been separated from each other.

The deductions I have arrived at in this paper are based on a personal examination and comparison of the following specimens:—

A. A very young (and, according to Haast, a male) skull, with its mandible,—one of three specimens sent from the Chatham Islands to Sir Julius von Haast in 1875. It is a co-type of *Mesoplodon* (*Oulodon*) *grayi*, Haast, described in vol. ix. of the 'Transactions' of the N.Z. Institute. In this specimen the vomerine trough is quite empty. It forms part of the collection in the Otago Museum, Dunedin, N.Z.

A*a*. A young specimen in the Otago Museum, Dunedin, in